Impacts of a specialist diet on aardwolf ecology

By

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Declaration

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Impacts of a specialist diet on aardwolf ecology

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Abstract

The diet of an animal plays a fundamental role in its ecology, and the consequence of a specific diet may be more pronounced in mammals with a specialised diet that are more reliant on a specific food type. This can have a dramatic effect on its activity patterns, home range size and the interaction with heterospecifics. Investigating the diet of specialist mammals and the subsequent effects it will have on their ecology is thus vital to the management and subsequent conservation of the species, and crucial to our understanding of how the animal can survive and reproduce. In this thesis I investigate the effect that the diet

of the aardwolf, a highly specialised myrmecophage, has on its ecology. Aardwolves feed predominantly on one genus of termite, *Trinervoides* spp., and are thus extremely dependent on the abundance and distribution of this arthropod. I firstly investigated the effect of temperature and rainfall on arthropod abundance and diversity, and further investigated the variation of arthropod abundance and diversity across the four habitat types at study site. This is one of a few studies that have been conducted on arthropod abundance and diversity in an arid environment and the findings show that in an arid environment arthropods are mainly influenced by temperature rather than rainfall. This is in contrast to studies in temperate and forest habitats where rainfall is the most important abiotic factor determining the abundance and diversity of arthropod assemblages. Habitat type still plays a major role in the abundance and diversity of arthropods, and habitat types that are more complex and diverse have both a higher diversity, and abundance of arthropods than other habitats. Due to the absence of prey items during the colder months of the year I investigated the diet of aardwolves to see if they display a switch in diet. This included an investigation into the seasonal variation of diet from a detailed scat analysis, using a newly developed method to assess scat content. The analysis of scats revealed that, contrary to previous studies, aardwolves showed no switch in diet and continued to feed on *Trinervitermes*. Using the data from the scat analyses and the information from the abundance and diversity of arthropods at the study site I expanded the study to investigate the functional responses of the aardwolf to change in prey abundance at the locality. Aardwolves demonstrate a Type I functional response to changes in prey abundance, a response that is normally found in plankton feeders. The expected functional response for specialist animals would be Type II response, and I propose that the Type I response seen in aardwolves is probably as a result of a limited handling time which reduces time spent foraging. The abundance of termites thus had a clear effect on the diet of aardwolves, showing that they feed on fewer when they are unavailable, and as such I

investigated the effect of termite densities on home range sizes. The number of termite mounds in a home range influenced the size of the home range, and aardwolves with larger home ranges had a lower density of termite mounds. In contrast to previous studies, large overlaps between neighbouring individuals were recorded and indeed three male aardwolves shared a common den. I propose that the reason behind the overlap of home ranges is that a higher prey abundance during my study period occurred and as a consequence aardwolves did not need to defend an area to protect this resource. *T. trinervoides* has thus played a keystone role in driving the biology of the aardwolf and shaping many aspects of its ecology.

Keywords: Aardwolf, termites, specialist mammals, feeding ecology, arthropods, home ranges, scat analysis, functional responses

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Disclaimer

Chapters 2, 3, 4 and 5 of this thesis have been prepared for submission to different scientific journals. Therefore, styles and formats may vary between all chapters of this thesis and some overlap in content may occur throughout the thesis to secure publishable entities. Other authors are included in the chapter reference, listed on the first page of the chapter. For each chapter, my input was the greatest, as I planned the research, undertook the field work, analysed the data and wrote the manuscripts. I was helped by my co-authors, who were my supervisors.

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~ Chapter 1 ~

General introduction

Dietary strategies are fundamental to an animal's ecology and influences a wide spectrum of behaviours exhibited by the organism (Futuyma & Moreno 1988). Based on the dietary strategy used, animals may be broadly defined as either generalists or specialists, with generalist feeders incorporating a wide diversity of food commodities in their diet, whereas specialists feed on relatively few taxa (Shipley, Forbey & Moore 2009). Dietary specialisation is a much less common strategy used by mammals than generalist feeding, and has in turn further been categorised, into facultative and obligatory specialisation (Glasser 1982, Shipley, Forbey & Moore 2009). Facultative specialists feed on one taxon of prey, such as a specific arthropod taxon or plant item, but have the ability to switch to a more abundant food type when their preferred food becomes limited (Malo *et al.* 2004). These animals will thus show variation in diet across a spatial and temporal scale depending on the abundance of food resources. Obligatory specialists on the other hand show little or no variation of food types consumed and seem unable to switch to another food type when the dietary resources they specialise on becomes limited (Shipley, Forbey & Moore 2009). As such, obligatory specialisation appears to be an evolutionary unstable dietary strategy and it is not intuitively clear how such a strategy may have evolved. If these animals do not have the ability to feed upon other prey types they will be vulnerable when their preferred food become limited or scarce (Terraube *et al.* 2012).

Facultative specialists thus have a broader range of prey items available to them throughout the year compared with obligatory specialists. Previous studies on dietary specialists have reported that variation in the availability of prey items may cause a shift in both home range size and use (Joshi, Garshelis & Smith 1997). The reliance of obligatory specialists on a limited number of taxa of prey results in the regulation of home range size and its use according to the availability of the specific prey items in the area, whereas facultative specialists are able to accommodate variation in prey abundance by switching to another item and as a consequence do not have to regulate their home range size or use so religiously (Gittleman & Harvey 1982, McNab 1963). Many prey types, such as arthropods (Barrow & Parr 2008, Janzen & Schoener 1968), are seasonally active, and understanding how prey items vary in abundance both across time and space is thus important for the assessment of how alternative prey items may be incorporated into the diet.

Myrmecophagy (consumption of ants and termites) has been recorded in 216 mammalian species from 13 orders and is thus a fairly common dietary strategy. True myrmecophages are defined as species whose diet comprises of at least 75 % of ants, termites or a combination of the two prey items and has been found in only 44 species from 10 orders (Redford 1987). Specialist myrmecophages (where diet that consists at least 90 % of ants and termites) are rarely found, and this has only been recorded in 12 species from six orders (Redford 1987).

Ants and termites fall below the suggested prey size for many myrmecophagous mammals to sustain themselves energetically. Predictive modelling has suggested that when a mammal weighs 10 kg or above it cannot sustain itself by feeding solely on prey items that are significantly smaller than itself (Carbone *et al.*

1999, Carbone, Teacher & Rowcliffe 2007). Moreover, since ants and termites are often not active during the dry season myrmecophages will be under additional energetic stress at these times of the year (Dawes-Gromadzki & Spain 2003, Braack 1995, Lindsey & Skinner 2001). Energetic constraints such as these may be alleviated by a mammal lowering its metabolic rate (giant ant-eater, *Myrmecophaga tridactyla*)(Mourão & Medri 2007) or by switching the diet to different termite or ants species when the staple food prey becomes scarce (aardwolf, *Proteles cristata*) (Richardson 1985). Due to the energetic constraints resulting from the consumption of small prey items, myrmecophages thus provide us with an ideal model to investigate the causes and consequences of dietary specialisation which in turn reduces metabolic rate (McNab 1984, Cooper & Withers 2002, Best & Harada 1985).

Even though myrmecophages do not consume vertebrate prey due to vestigial dentition (Anderson & Jordaan 1991) it has been shown that they are capable of feeding on arthropod prey other that ants and termites (de Vries *et al.* 2011, da Silveira Anacleto 2006). This poses a conundrum, if these animals are capable of feeding on a wide variety of prey, why do they concentrate their feeding on ants and termites? Even though these animals are able to feed on other arthropod prey types they continue to concentrate feeding on, what seems to be for many, a suboptimal prey item due to energetic constrains. The extent to which these mammals feed on ants and termites seems to vary with the geographical and ecological variation of ants and termites, but individual preference plays a prominent role (Redford 1986). The aardwolf, being an myrmecophage specialist (Richardson 1987a, de Vries et al. 2011), provides us with the opportunity to investigate if they will switch to alterative prey when this prey is limiting and how such a myrmecophageous diet influences their home range size.

The aardwolf is the smallest member of the family Hyaenidae weighing between 8 and 12 kg (Koehler & Richardson 1990). The diet of these hyaenids has been thoroughly investigated and it has been shown that they feed almost exclusively on one genus of termite, *Trinervitermes* (Cooper & Skinner 1979, Bothma, Nel & Macdonald 1984, Matsebula *et al.* 2009, Richardson 1987b, de Vries et al. 2011, Kruuk & Sands 1972). These studies have led to the conclusion that aardwolves are one of the most dietary specialist mammals in Africa and they thus present us with a perfect model to investigate specialisation (Richardson 1987a). Previous studies have been carried out to investigate aspects such as home range size (Sliwa & Richardson 1998, Skinner & van Aarde 1985), mating patterns and den use (Richardson 1991, Richardson & Coetzee 1988, Kotze *et al.* 2012) and the metabolism (Williams, Anderson & Richardson 1997).

Termites are not of high nutritional value and during the colder months they are relatively inactive (Redford & Dorea 1984). The high level of dietary specialisation by the aardwolf allows for evaluation of the relationship between home range size and prey abundance. Aardwolves rely on one prey item that essentially dictates the size of home range. Interestingly, aardwolf home range and body size have never been compared with other myrmecophages (Gittleman & Harvey 1982).

Aardwolves, being the best studied myrmecophage in southern Africa, provides us with a good model on which we can build further on our knowledge of other myrmecophages in southern Africa and the rest of the world. In addition, research has shown the importance of repeating studies (Ioannidis 2005). As such, not only will the aardwolf provide us with insights into the ecology and lifestyle of myrmecophages, but it also gives us the opportunity to revisit previous studies and assess the findings in light of the original ideas presented in this thesis.

2. An overview of mammalian myrmecophagy

A possible reason for the rarity of mammalian dietary specialisation on ant and termites is that they are energetically sub-optimal as a prey item for large vertebrates (Carbone et al. 1999). Although myrmecophages, such as the silky ant eater (*Cyclopes didactylus*) are small enough for ants and termites to be energetically profitable as prey (Best & Harada 1985), in many other species they exceed the size limit for which ants and termites are predicted to be able to sustain them energetically (Carbone et al. 1999). Many, such as the giant ant-eater, have a reduced metabolic rate, whereas others, such as the numbat, (*Myrmecobius fasciatus*) have the ability to enter into bouts of torpor (McNab 1984, Cooper & Withers 2002), while the aardwolf undergoes a loss of body mass during the colder months (Anderson 2004). Myrmecoophages tend to have smaller home ranges than would be predicted for their body size (Nicol *et al.* 2011), and reduce their activity during the coldest or hottest parts of the day to minimise energy expenditure (de Sampaio, Camilo-Alves & de Miranda Mourão 2006).

Myrmecophagy is generally considered more common among phylogenetically older mammals (McNab 1988, Uys 2002, Seymour & Dean 1999, Cheli *et al.* 2010). However, specialised myrmecophages are still phylogenetically diverse and includes species such as the basal short-beaked echidna (*Tachyglossus aculeatus*) from the subclass Prototheria through to carnivores from the subclass Eutheria (Redford 1987, Redford 1986). One order of mammals, the pangolins (Pholidota), evolved relatively recently (Tobe, Kitchener & Linacre 2010) and all members of this order are specialist myrmecophages. Thus even though myrmecophagy is more common in early mammals it is not restricted to these individuals and seems to be a strategy that is employed widely in mammals.

Although myrmecophagy is an uncommon feeding strategy in mammals, myrmecophages are widely distributed around the world. In Australia the short-beaked echidna, the marsupial mole (*Notorectes typhlops*) and the striped possum (*Dactylopsila trivirgata*) are ant-specialists, whereas the numbat (*Myrmecobius fasciatus*) is a termite-specialist (Abensperg-Traun & Steven 1997). Many other Australian mammals consume ants and termites to some extent, but in lower quantities.

South America boasts a large diversity of ant and termite eaters within the super order Xenartha. Most of the armadillos (Dasypodidae) have been poorly studied, and for the most part, little is known about their diet. Many of the armadillos feed on ants and termites to a large extent, but all species consume other invertebrates or plant material as a large part of the diet, or supplement their diets with other prey (da Silveira & Anacleto 2006, Abba, Cassini & Galliari 2011, Abba *et al*. 2011). The ant-eaters (families Cyclopedia and Myrmecophagidae) are more specialised and feed almost exclusively on ants (Lubin & Montgomery 1981, Best & Harada 1985, Mourão & Medri 2007)

In the northern parts of Africa, the only mammals that are known to specialise on ants and termites are eight species of pangolins (Manidae) and a few species of elephant shrews (*Elephantulus* spp.) are reported to feed on ants and termites (Swart, Richardson & Ferguson 1999, Lim & Ng 2008, Skinner & Chimimba 2005). Little has been done on these enigmatic animals, and only the Chinese pangolin (*Manis pentadactyla*), which is one of only three myrmecophage in Eurasia, and the tree pangolin (*Manis tricuspis*) of Africa have been well investigated (Lim & Ng 2008). In southern Africa there are a few more mammals that make use of termites and ants as a part of their daily diet. Among these are the Cape pangolin (*Manis temmincki*), the aardvark (*Orycteropus afer*), Meller's mongoose (*Rhynchogale melleri*) and the aardwolf (Taylor, Lindsey & Skinner 2002, Skinner & Chimimba 2005, Swart, Richardson & Ferguson 1999, Richardson 1987b). The bat-eared fox (*Otocyon megalotis*) also feeds on termites on a regular basis, but based on more recent research it would appear that termites are not as important as was originally suggested with the diet of the bat eared fox actually being more catholic (KlareKamler & Macdonald 2011).

3. The aardwolf, *Proteles cristata*, (Sparrman, 1783): an overview.

3.1 Taxonomy

While initially incorrectly classified as a grey jackal until subsequent examination of the dentition, the aardwolf was initially classified as *Viverra cristata* (Sparrman

1783), the aardwolf was subsequently placed in its own family, Protelidae, but it is now regarded to be the most recently evolved member of the extant hyaenids (Koepfli *et al.* 2006, Simpson 1945). This classification has been confirmed by genetic studies (Wurster & Benirschke 1968). However, the distinctive dentition and an extra digit on the front foot have resulted in the placement of it in the sub-family, Protelinae (Koepfli et al. 2006)

3.2 Morphology and anatomy

The aardwolf is a medium-sized carnivore weighing between 8 and 12 kg (Fig 1, Koehler & Richardson 1990). It is the smallest extant member of the Hyaenidae with which it shares the characteristic sloped back and anal gland used for scent marking (Skinner & Chimimba 2005, Koehler & Richardson 1990, Richardson 1991). The canines are well-developed, but the rest of the dentition is severely reduced, with small, vestigial peg-like molars (Fig 2, Skinner & Chimimba 2005). It is speculated that the aardwolf masticates its food primarily using the enlarged pyloric region of the digestive system, and in this way releases a minimum amount of the terpenoids, that are secreted by their main prey (*Trinervitermes* spp), into its mouth (Anderson, Richardson & Woodall 1992). The tongue is very broad and covered with hardened papillae which, with the aid of enlarged salivary glands, allows the aardwolf to lap up and swallow termites without chewing them (Fig 1, Anderson, Richardson & Woodall 1992). Licking up termites from the ground in this fashion is unusual for a myrmecophagous mammal since most will break open mounds and feed on termites in the nests (Redford 1986)

Figure 1. Photograph of a collared female aardwolf foraging. Inserted in the top left corner is a picture of an aardwolf's tongue showing the spatulate tongue with papillae visible. Photographs by J.L. de Vries

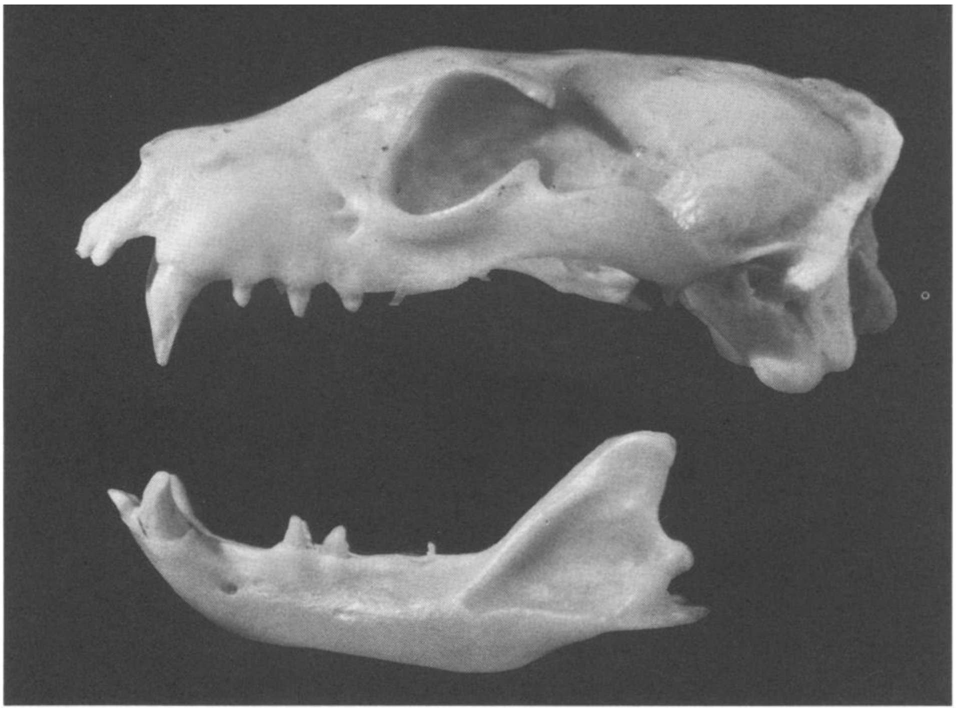

Figure 2. Lateral view of the skull of an aardwolf indicating the reduced dentition. Photograph by B. Boyle (Koehler & Richardson, 1990).

3.3 Diet

Aardwolves feed predominantly on termites of the genus *Trinervitermes* and supplement the diet by feeding on *Hodotermes* (Richardson 1985). This makes the aardwolf the most specialised of the African carnivores (Cooper & Skinner 1979, Bothma, Nel & Macdonald 1984, Kruuk & Sands 1972, Matsebula et al. 2009, Richardson 1987b, de Vries et al. 2011, Richardson 1987a). *Trinervitermes* spp. are common and widely distributed throughout southern Africa, with their occurrence confirmed by large epigeal mounds (Uys 2002). An important characteristic of

Trinervitermes is the lack of pigmentation in the exoskeleton (Hewitt, Nel & Schoeman 1972, Sands 1965), making them susceptible to UV light which forces them to forage at night. Aardwolves are primarily nocturnal, foraging and feeding on these termites which appear at night (Richardson 1985). *Trinervitermes* are also highly sensitive to cold temperatures and are usually not active at the temperatures below 13 °C (Richardson 1985). Consequently, during the winter months aardwolves feed more on the partly diurnal *Hodotermes* to compensate for the lack of surface-active *Trinervitermes* (Richardson 1985).

Soldiers of *Trinervitermes* secrete a highly noxious terpentine cocktail as a defence mechanism which no other mammal, besides the aardwolf, can consume in high quantities (Richardson 1987a). Due to the aardwolves' specialisation on these termites, and their ability to deal with the high concentration of terpenes they probably experience limited or no competition over this food resource from other mammals. Although aardvarks are known to open *Trinervitermes* mounds to feed on termites (Shoshani, Goldman & Thewissen 1988), it is suspected that benefit from the opened mounds by feeding at them when the aardvarks are done (Taylor & Skinner 2000).

3.4 Distribution

Aardwolves occur in the southern and eastern part of Africa, ranging from South Africa through into Egypt. There is an absence in their distribution for about 1 500 km across much of Mozambique and a large part of Tanzania. Two subspecies occur on either of this divide, *P. c. septentrionalis* in the East and *P. c. cristata* in the South (Fig 3).

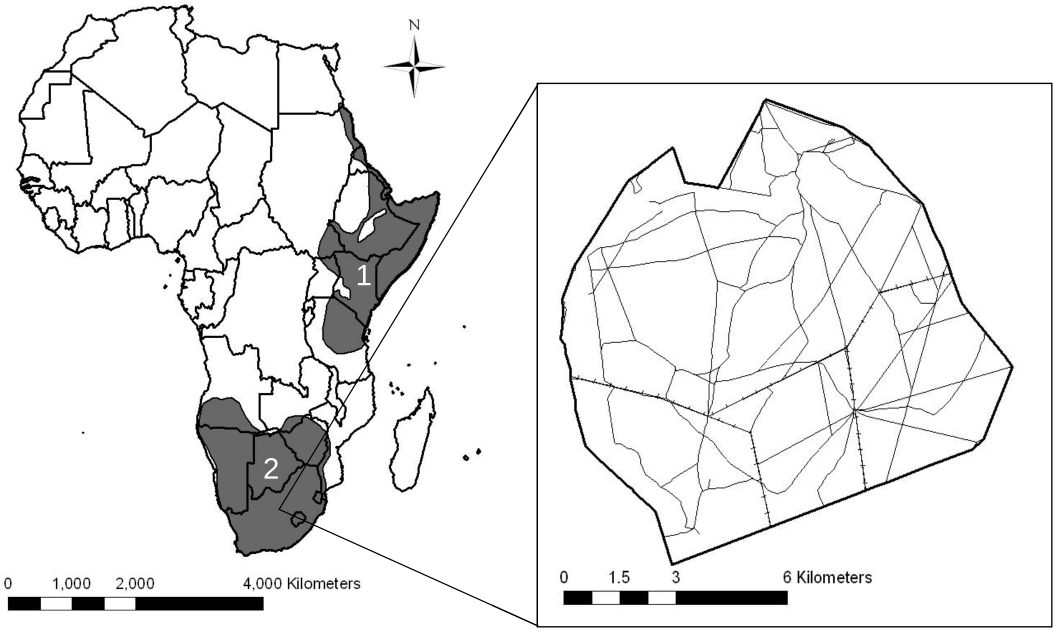

Figure 3. Distribution of the aardwolf across Africa with insert of the study side, Benfontein Game Reserve. Map indicates the distribution of the two subspecies; 1) *P. c. septentrionalis* which occurs in eastern Africa and 2) *P. c. cristata* which occurs in southern Africa.

4. Study site

This study was conducted at Benfontein Game Reserve (28°50’S, 24°50’E) in the Northern Cape Province of South Africa (Fig 1). The reserve is 11 000 ha in size and situated where the Kalahari thornveld and Karoo meet (Acocks 1988), and it contains four different habitat types, namely savanna, grassland, shrubland and pan. There is considerable overlap between habitat types that are geographically close to one other. The savanna is the only area with trees and is mainly dominated by *Acacia erioloba* and two species of grass, *Stipagrostis uniplumis* and *Eragrostis lehmanniana*. There is a large overlap in plant composition between the grassland and the shrubland with *Pentzia* species and various species of grass occurring in the area. The pan is covered by *Salsola exalata* and *Suaeda fruticosa* shrubs but these are frequently intersected by open areas (Richardson 1985).

The reserve has a semi-arid continental climate with cold and dry winters (Schulze & McGee 1978), where minimum temperatures may drop to below freezing point at night and normally stay below 20°C during the day (South African Weather bureau). Very little, if any, rain falls during these months. The summer months are hot and wet, with temperatures reaching into the high 30’s. Thundershowers are common during the summer months. Rainfall varies greatly with the wettest month receiving close to 120 mm of rain and the driest month receiving no rain (Fig 4).

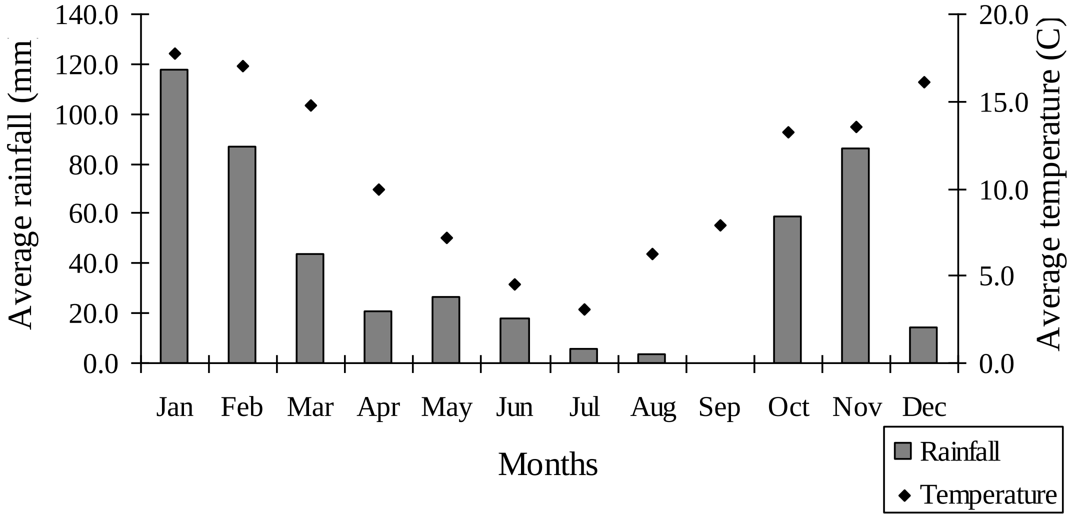

Figure 4. Average monthly rainfall and minimum temperatures for the two year period during which the study was conducted.

5. Key questions and thesis outline

The aim of this thesis was to investigate the relationship between aardwolves and their main prey source, *T. trinervoides*, in order to determine what impact the distribution and densities of termites have on the diet and home range of aardwolves. With this knowledge I will be able to make suggestions with regards to how other obligatory specialists behave when faced with variations in prey abundance. The subsequent information obtained will enlighten us as to how animals that are so specialised might behave if threatened by a reduction in prey abundance. I asked four questions to aid in the understanding of the relationship between aardwolves and their food source.

Question 1: How do different habitat types and seasons affect the abundance and diversity of arthropods on Benfontein Game Reserve?

In Chapter 2 I investigate the variation of arthropods across spatial and temporal scales at the study site to determine how potential prey items for aardwolves vary across time and space. Such data provide information about the variation in the abundance and diversity of invertebrate prey communities with may act as alternative prey items for aardwolves. I used pitfall traps in each of the four habitat types during both the wet and dry season to test for variation in the activity patterns of arthropods and identify the differences in arthropod communities between habitat types.

Few studies have been done on arthropod diversity and abundance in arid regions, making this chapter more than just an investigation into the prey available to aardwolves. This chapter also provides valuable information about arthropods in the arid regions of southern Africa.

Question 2: How does aardwolf diet vary in response to temporal variation in the abundance of alternative prey items?

Aardwolves are predicted to be energetically stressed during the winter months unless they switch prey type. In Chapters 3 and 4, I investigated seasonal variation in the diet of aardwolves through scat analyses. In Chapter 3 I report prey items other than *Trinervitermes* that have been reported on very few occasions in the diet of the aardwolf or for the first.

In Chapter 4, I focus on how aardwolves use alternative prey items in relation to seasonal variation in their abundance. This is achieved by comparing the relationships between the dietary importance of the most common prey categories (estimated from the scat analyses) and their abundances (estimated from the pitfall traps) to functional response curves that each represents a specific dietary strategy.

The functional responses of myrmecophages have never been investigated making this the first study of its type.

Question 3: What is the effect of prey abundance on aardwolf home range sizes?

In Chapter 5, I investigate if aardwolves adjust their home range sizes according to the abundance of their main prey *Trinervitermes trinervoides*, by evaluating the relationship between home range size and termite mound density. I also compare how aardwolf home range size scales with body size compared to other myrmecophages.

The impact of prey abundance on aardwolf home range size and use has not been investigated since telemetry equipment has been available making this study more accurate than previous studies. I also use software previously unavailable to determine prey density. This study will thus be more comprehensive and provide greater insights into aardwolf home range size than any previous study.

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~ Chapter 2 ~

Variation in arthropod diversity and abundance across spatial and temporal scales in the arid Northern Cape Province of South Africa.[+]

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Abstract

Arthropods are the most widely distributed taxa of animals on the planet, and yet studies on the diversity and abundance from arid environments are generally lacking. The abundance and diversity of these animals varies widely across the world due to variation in habitat structure and seasonality. Arthropods tend to be more abundant in areas where plants, and the structure of plants, are more diverse; they are also more abundant during the wet season. In this chapter we investigate the alpha and beta diversity as well as the abundance of arthropods from an arid environment in South Africa with four different habitat types and across two seasons using pitfall traps. Arthropod diversity and abundance was greater in habitats (savanna and grassland) that had more plant species than in the habitat types with fewer species (shrubland and pan), and season had a distinct influence on both the abundance and diversity of arthropods with them being higher during the wet season than during the dry season. This result is in accordance with studies conducted in temperate and forest environments however, contrary to these studies we found that lower temperature rather than rainfall affected the diversity and abundance negatively. This finding suggests that in arid environments it is temperature, rather than rainfall, that has the greatest influence on the abundance and diversity of arthropods.

Introduction

Diversity encompasses a broad range of scales from the species level up to global biomes (Hooper *et al.* 2005). Although the exact definitions of the various components of ecological diversity are being refined (Jurasinski *et al.* 2009; Moreno and Rodríguez 2010), alpha diversity is designated as the diversity of organisms within a specific site in an area whereas beta diversity is the difference in diversity between these sites. Gamma diversity is defined as the overall diversity of all the sites sampled in a specific area (Tuomisto 2010).

The phylum Arthropoda is the most diverse extant phylum of living animals with an estimated species richness of between 5 and 10 million species (Ødegaard 2000). Since arthropods are both abundant and relatively easy to sample, they provide an opportunity to test how factors such as habitat and climatic variables influence diversity. The diversity and abundance of arthropods in a habitat has consequences not only on plants through top-down processes, but also as a food source through bottom-up processes (Walker and Jones 2001; Ødegaard 2000). Consequently, many studies have investigated arthropod diversity and both the factors that influence that diversity and the effect the diversity has on ecosystems (Buskirk and Buskirk 1976; Dingle and Khamala 1972; Hails 1982; Janzen and Schoener 1968). However, most studies have focussed on tropical environments, whereas comparatively few have been conducted in arid or semi-arid environments (Godfray *et al.* 1999). This discrepancy is particularly prominent in Africa. Large parts of the continent are covered in desert and yet most studies have been conducted in the tropical areas. Studies in arid regions are thus needed to investigate if variation in climate and different habitat types will have the same effect on arthropod diversity as it has in tropical enviroments.

Plant diversity and the structure of vegetation influence the diversity and abundance of arthropods (Haddad *et al.* 2001; Southwood *et al.* 1979). Increased plant diversity in the community generally has a positive effect on arthropod diversity because a greater diversity of plant species supports more herbivorous arthropods (Siemann *et al.* 1998), which in turn results in a greater diversity and abundance of predatory and parasitic arthropods (Jonsen and Fahrig 1997; Siemann *et al.* 1998; Southwood *et al.* 1979). Increased plant diversity also creates a more variable environment with a greater number of refuge places and micro-niches for arthropods (Bennett 2010; Price *et al.* 1980). The floral characteristics of a habitat thus influence the abundance and diversity of arthropods by acting as a food source.

In addition to plant characteristics, seasonal change and associated climatic factors influence the abundance and diversity of arthropods (Barrow and Parr 2008; Boyer *et al.* 2003; Denlinger 1980; Wolda 1988). The effect of season in arid and tropical areas has mainly been attributed to variation in rainfall (Wolda 1988). As a consequence, seasons are often referred to as 'wet' or 'dry' (Janzen and Schoener 1968; Vasconcellos *et al.* 2010). In the arid region of South Africa reduced rainfall negatively affects plant growth in grasslands and savanna (Milton and Dean 2000; O'Connor 1994), and reduced plant growth is likely to have negative effects on arthropod abundance (Haddad *et al.* 2009; Southwood *et al.* 1979; Srivastava and Lawton 1998).

Understanding the variation in arthropod abundance and diversity in different habitat types can lead to a better understanding of the insectivores that occurs in that area. Considering the lack of studies conducted in arid environments and the number of insectivores occurring on our study site alone, investigations such as these have implications on more animals than just the arthropods in the area.

In this study we investigated the effects of habitat type and season on arthropod diversity and abundance in an arid sandveld environment of the Northern Cape Province of South Africa. We predicted that habitat type and climatic variables will have an influence on both the diversity and abundance of arthropods as this has been concluded in previous studies done, even if these studies were mostly conducted in tropical areas. We predict that the habitat types that are structurally more complex will provide more cover and refugia, and therefore will have a higher diversity and abundance of arthropods. More arthropods should also be present, and the diversity should be higher, during the wet season than during the dry season since arthropods are more active during wet seasons. These predictions were investigated by determining I) seasonal and habitat variation in within habitat diversity of arthropods (i.e. alpha diversity); II) habitat and seasonal variation in arthropod diversity between sites within and between different habitat types (beta diversity); III) habitat and seasonal variation in the relative abundance of arthropod orders; IV) the effects of rainfall and temperature on abundance and diversity of arthropods, and how such climate effects varied between habitats.

Materials and methods

Study site

The study was conducted on Benfontein Nature Reserve, which is situated 10 km south of Kimberley in the Northern Cape province of South Africa (28°50’S, 24°50’E). There are four distinct habitat types present on the reserve namely savanna, grassland, shrubland and pan (Fig 1). The savanna is located in the south-eastern part of the reserve and is dominated by two species of grass, *Stipagrostis uniplumis* and *Eragrostis lehmanniana*, and one tree species, *Acacia erioloba*, with *Ziziphus mucronata* being the only other tree species that occurs in high numbers. A few shrubs such as *Protasparagus laricinus*, *Lycium hirsutum* and *Chrysocoma tenuifolia* occur in this area. This is the only habitat on the reserve where trees occur in abundance. This area is characterised by very sandy soil.

The grassland habitat is situated in the eastern part of the reserve, runs through the central part and stretches to the south-western section of the reserve. The two most common grasses are *Cymbogon plurinodis* and *Panicum stapfianum*. Less common species include *Enneapogon desvauxii, Tragus koeleroides* and *Eragrostis lehmannians* with the karroid shrub *Pentzia incana* growing amongst the grasses. The grassland area surrounding the savanna is a mixture of *Stipagrostis uniplumis* and *Eragrostis lehmannian*.

The shrubland habitat is characterised by three *Pentzia* species (*P. spinescens, P. calcarea* and *P. incana*), *Sporobolus ludwigii* and *Rosenia humilis*. A few other shrubs and succulents such as *Walafrida saxatius* and *Salvia verbenaca* also occur in this habitat. The soil in the grassland and shrubland varies between fine sandy soil and calcareous soil with more grassland on the sandy soil and the calcareous soil being more characteristic of the shrubland.

The majority of the pan habitat is covered by *Salsola exalata* and *Suaeda fruticosa* shrubs but these are frequently intersected by open areas. Another shrub that occurs on the pan is *Psilocaulon articulatum* and there are a few grasses such as *Eragrostis bicolor*, *E. truncata* and *Lycium horridum*. The entire area has a clay-rich soil with high salinity and during the rainy season a large part of this area retains water for weeks. During the dry season the soil is baked hard by the sun.

Benfontein has a semi-arid continental climate (Schulze and McGee 1978). The winter months are cold and dry with temperatures dropping below 5^{o} C at night and staying below 20^{o} C throughout the day during July, the coldest month of the year. The summer months are hot, and temperatures vary between 14^{o} C and 35^{o} C (South African Weather Bureau). During these months temperatures may rise into the high thirties. The winter months are dry with little to no rainfall with the peak annual rainfall falling during autumn. The area has a mean annual rainfall of 431 mm (1 SD 127 mm) (Richardson 1985). During the duration of our study, most rain fell during January (average 118mm ± 1sd 25.7) with September being the driest month with no rain. We used rainfall to classify sampling events into wet and dry season based on data received from the South African Weather Bureau, with a mean precipitation of less than 40 mm per month (April – end September) being defined as dry season, with the wet season spanning October until the end of March.

Pitfall traps and arthropod identification

Pitfall traps were set at monthly intervals at six sites in each of the four habitat types (Fig. 1) and left open for a period of one week between July 2008 and

December 2009. At each site, three pitfall traps were placed within 1 m of each other for a total sampling effort of 72 traps per month. Each trap was 1/3 filled with a 2:1 mixture of water and propylene glycol. Each trap had a diameter of 6 cm and was dug into the soil, placed flush with the surface. When the pitfall traps were collected and emptied all arthropods were stored in 70 % ethanol.

Every individual of all arthropod specimens was counted and identified to the level of order. Diplopoda and Chilopoda were identified to class and the Acari were identified to subclass.

Statistical analyses

The method used to analyse diversity is highly context dependent, but multivariate statistics are more suitable for quantifying alpha and beta diversity than univariate methods (Jurasinski *et al.* 2009; Tuomisto 2010).

We quantified alpha diversity within each habitat type and season with the Shannon-Wiener index of diversity (Shannon 1948). The Shannon-Weiner index is expressed as an H-score which is based on the degree of heterogeneity of the data, with the index value increasing with increasing heterogeneity. We determined the H-scores for each trap with a subsequent Mixed Model using a Guassian distribution. We fitted full models including all interaction terms as well as sample month blocked over trap nested within site nested within habitat as random effects. Sequential likelihood ratios tests were used to test if rainfall, temperature or habitat significantly influenced alpha diversity. Interaction terms between the three factors were included.

These models where done twice, once with ants included and once with them excluded from the analysis in order to determine the effect of ants on alpha diversity.

We quantified the beta diversity between habitats and between sites within habitats as Euclidean distances from each trap to the group centroids in a multidimensional space defined by the detected taxonomic groups (Anderson *et al.* 2006; Oksanen *et al.* 2011). To compare beta diversity within and between habitats, we calculated Euclidean distances both to trap site centroids and to habitat centroids. We calculated the Euclidean distances on raw counts of individual arthropods from each taxonomic group for each trap. Subsequently linear mixed models were fitted to estimate the impact of temperature, rainfall and habitat on beta diversity using a Guassian error family and a log link function. This was done using habitat and site Euclidean distances with ants included and excluded from the analysis. A type 2 ANOVA was used to test for significant influences. A Tukey HSD test was performed to test for significant differences between habitats.

A mixed model was fitted to the raw count data from the each of the pitfall traps evaluating the effects of temperature, rainfall and habitat type on the relative abundance of all taxonomic groups of arthropods. The models included all interaction terms as well as sampling month blocked over trap nested within site nested within habitat as random effects, using a Guassian error family and a log link function. The significance of fixed effects was evaluated by sequential likelihood ratios tests. As with alpha and beta diversity this analysis was conducted with ants included and excluded from the analysis.

Similarity percentages (SIMPER) analyses were conducted which gave an indication as to how similar each habitat is to another one during both seasons. This analysis was conducted with PRIMER software version 5.2.0.

We calculated the Shannon-Weiner indices and conducted the SIMPER analyses using the software PRIMER version 5.2.0 (PRIMER-E Ltd, 2001). All other analyses were conducted using the statistical package R version 2.13. (Bates *et al.* 2008) The Euclidean distances used for beta diversity analyses were calculated using functions in the user contributed R-package Vegan for R version 2.13.1 (Oksanen *et al.* 2011). Both the GLM's and the GLMM's were analysed using functions in the user contributed package lme4 (Bates *et al.* 2012)

Results

A total of 47 821 arthropods from 20 taxonomic groups were caught in the pitfall traps. Of these 73 % (34 989) belonged to Hymenoptera, of which 72 % (34 659) were ants. Therefore, ants were the most abundant and commonly trapped arthropod in all habitat types during both seasons.

Alpha diversity

Alpha diversity was higher during the dry season than during the wet season for all habitat types when ants were included in the analysis (Fig 2). The savanna had the highest diversity (wet season 1.04, ± 1sd = 0.2), dry season 1.46, ± 1sd = 0.13)) followed by the grassland (wet season 0.87, ± 1sd = 0.24 and dry season 1.30, ± 1sd = 0.26), shrubland (wet season 0.68, ± 1sd = 0.2 and dry season 1.16, ± 1sd = 0.25) and the interactions between habitat and rainfall affected the abundance and diversity of arthropods, where a less diverse habitat type and lower rainfall affecting arthropod diversity and abundance negatively (Habitat:Rainfall: χ^2=18.51, df = 17, p <0.05). Habitat and temperature also had a significantly negative effect on their own (Habitat: χ^2=10.24, df = 10, p <0.06; (Temperature: χ^2=14.1, df = 6, p <0.05). When ants where excluded from the analysis the only significant interaction was between habitat and rainfall significant (Habitat:Rainfall: χ^2=23.526, df = 17, p <0.05), whereas temperature on its own also significantly influenced alpha diversity (Temperature: χ^2=41.14, df = 6, p <0.05).

Beta diversity

For all habitats and seasons, there was higher beta diversity between than within habitat types (Fig 3). Only temperature and rainfall had a significant influence on beta diversity between habitats when ants were included in the analysis, with a lower abundance and diversity of arthropods found when temperature and rainfall was lower (Temperature: df = 1, F = 72.8207, p < 0.05; Rainfall: df = 1, F = 7.9553, p < 0.05). Beta diversity between sites within habitats was significantly influenced by temperature, habitat type and the interaction between temperature and rainfall when ants were included in the analysis (Temperature: df = 1, F = 52.7453, p < 0.05; Habitat: df = 1, F = 2.8981, p < 0.05; Temperature:Rainfall: df = 1, F = 9.5267, p <

0.05). When ants were removed from the analysis, temperature, habitat type and the interaction between rainfall and habitat had a significant influence on the beta diversity between habitat types (Temperature: $df = 1$, $F = 4.4662$, $p < 0.05$; Habitat: $df = 1$, $F = 26.0023$, $p < 0.05$; Rainfall:Habitat: $df = 3$, $F = 5.9698$, $p < 0.05$). Only habitat and the interaction between habitat and rainfall had a significant influence on beta diversity between sites when ants were excluded from the analysis (Habitat: $df = 1$, $F = 28.7299$, $p < 0.05$; Rainfall:Habitat: $df = 3$, $F = 6.5784$, $p < 0.05$). The difference between the wet and dry indicates that season has a significant influence on the beta diversity both within and between habitats (TukeyHSD: $df = 7$, $p < 0.05$). Beta diversity was always greater during the wet season than during the dry season. The presence of ants had no impact when comparing habitats during the same season, but had a significant influence when comparing habitats between the wet and dry season and within habitats (TukeyHSD: $df = 7$, $p < 0.05$). The only exception to this is the pan during the wet season. The pan only showed a significant difference when compared to the shrubland during the dry season but not to any other habitat type. However, when ants were excluded from the analysis no significant differences were observed between any of the habitat types. Lower rainfall and temperature always affected the diversity and abundance of arthropods negatively regardless of habitat type.

Arthropod abundance

The highest number of arthropods trapped was in the grassland during the wet season (127 per trap, Fig 4), but the highest number trapped in a specific habitat type was in the savanna (214 per trap, Fig 4). The pan had the lowest number of arthropods per trap during all seasons and also had the fewest arthropods overall (45 per trap during the wet season, 25 per trap during the dry season, 70 per trap overall). There were more arthropods trapped during the wet season than during the dry season in all habitat types except savanna, even when ants were excluded from the analysis (Fig 4).

There was a significant two way interaction between habitat and rainfall on the number of arthropods trapped (Habitat:Rainfall: $\chi^2 = 10.61$, df = 14, $p<0.05$). Habitat and temperature both affected the number of arthropods significantly (Habitat: $\chi^2 = 69.56$, df = 9, $p<0.05$; Temperature: $\chi^2 = 15.47$, df = 10, $p<0.05$).

The savanna and grassland showed the highest degree of similarity both when ants were included and excluded from the analysis (92.43 % & 91.01 %) whereas the savanna and pan showed the lowest degree of similarity (75.76 % and 75.61 %, Table 1). In all habitat types, ants contributed most to the differences between wet and dry season.

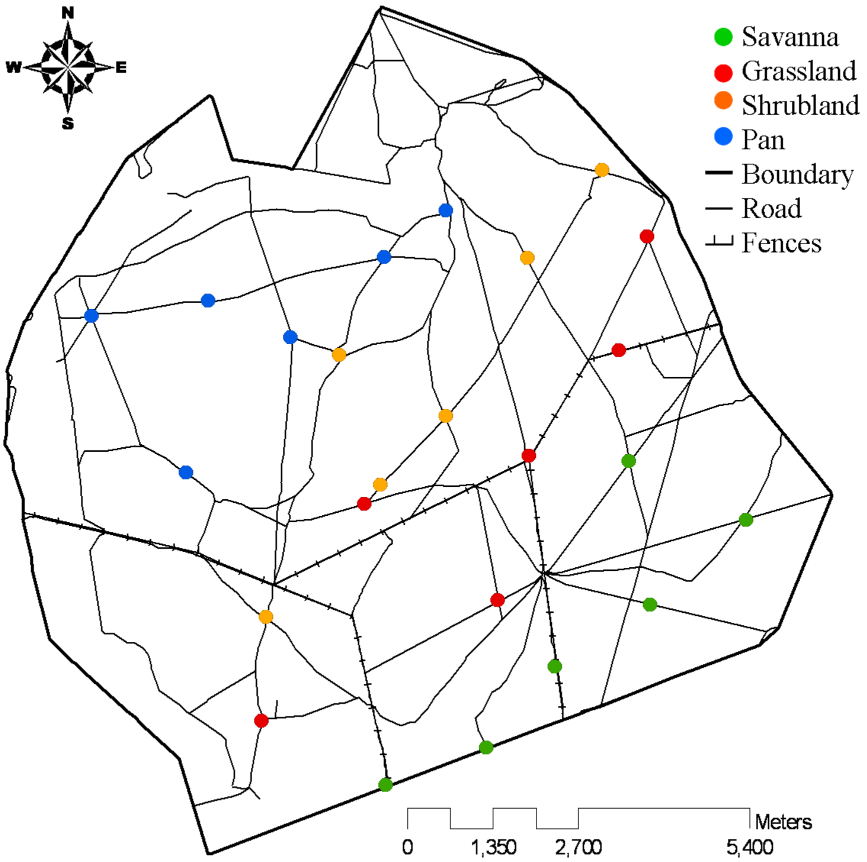

Figure 1. Map of Benfontein Game Reserve with coloured dots indication the locations of pitfall trap sites within each habitat type

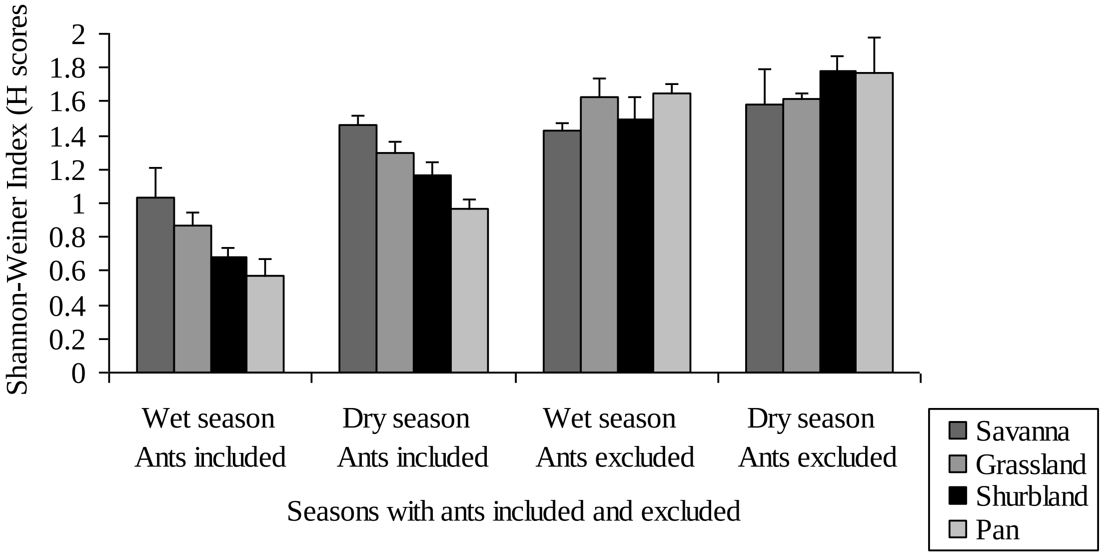

Figure 2. H score values for Shannon-Weiner diversity index when ants are included and excluded from the analyses indicating the level of heterogeneity between habitat types. Error bars indicate the standard error between sites within habitat types

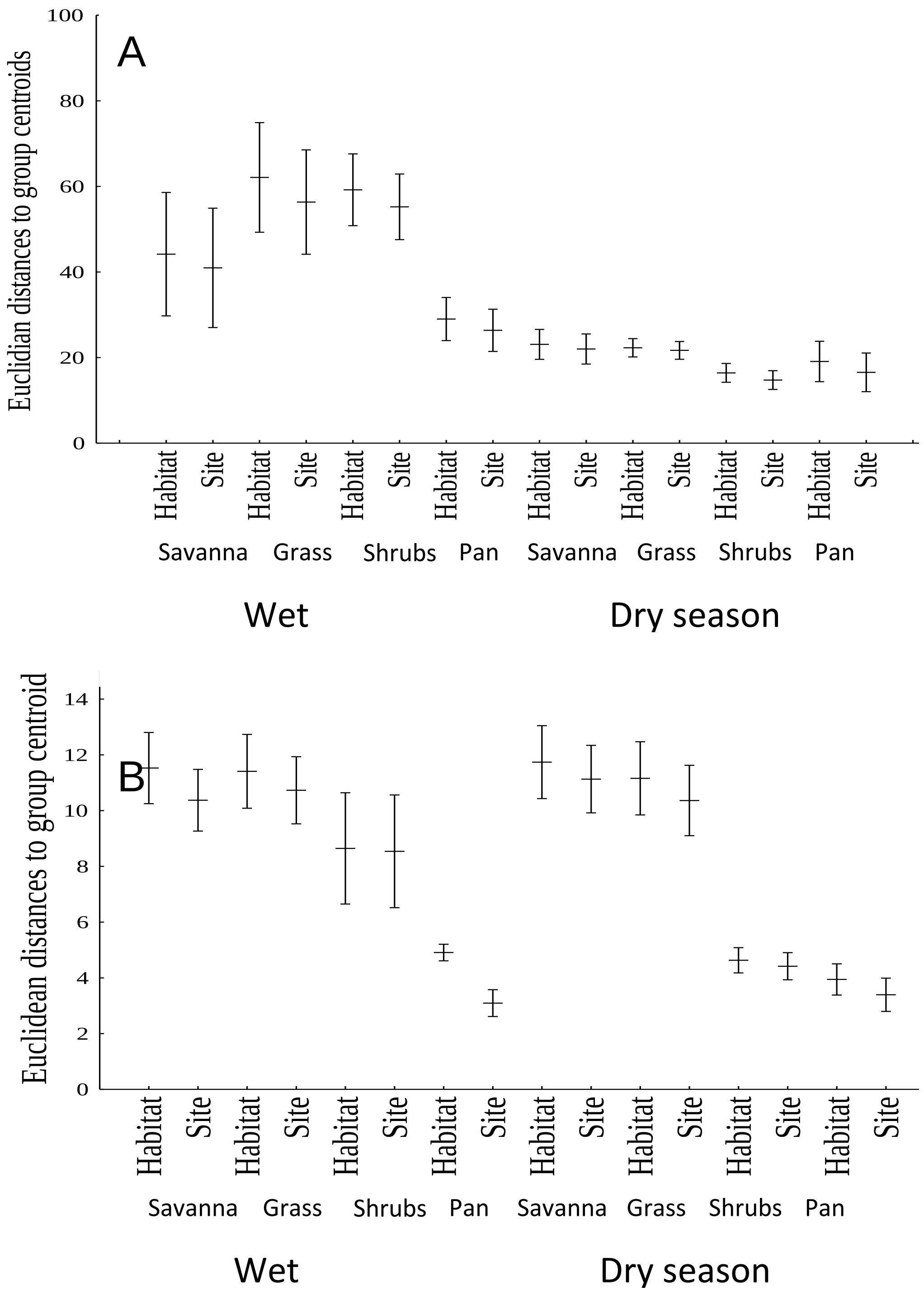

Figure 3. Euclidean distances to group centroids within each habitat type and between sites within habitat types displayed for the wet and dry season when ants are included (A) and excluded (B) from the analyses

Mean

— Mean ± SE

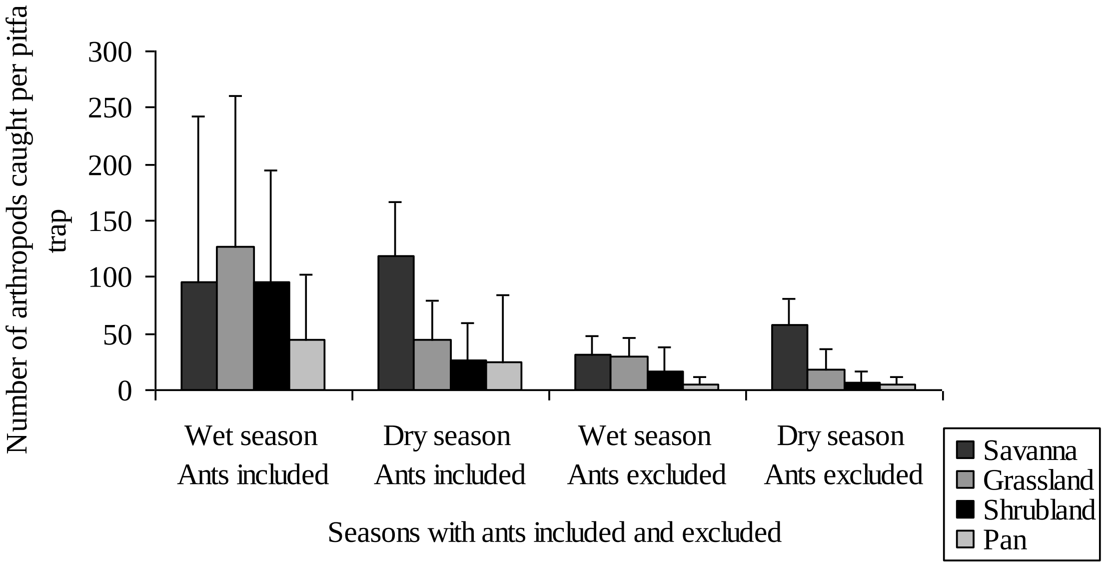

Figure 4. Mean number of arthropods captured in pitfall traps in each habitat type during the wet and dry season when ants are included and excluded from the analysis. Error bars indicates standard error.

	Ants present			
Ants absent	Savanna	Grassland	Shrubland	Pan
Savanna		92.43 %	82.68 %	75.76 %
Grassland	91.01 %		88.71 %	79.27 %
Shrubland	80.86 %	87.52 %		85.03 %
Pan	75.61 %	77.98 %	83.56 %	

Table 1. Percentage similarity (SIMPER) values between habitat types. The top section of the matrix presents SIMPER values when ants were included in the analysis whereas the bottom section presents values when ants were not included in the analysis.

Discussion

The savanna had the highest diversity of arthropods followed by the grassland, shrubland and lastly the pan with the lowest diversity. The savanna is the only habitat type with trees in addition to grasses and shrubs, and so presumably provides a wider and more complex range of vegetation types (Ríos-Casanova *et al.* 2006) as the trees create niches and refugia for herbivores that will not be found in the other habitat types where trees are absent (Jonsen and Fahrig 1997). The higher number of arthropod herbivores will in turn attracts more predators and parasites because more prey are available (Jonsen and Fahrig 1997). The grassland is dominated by various species of grasses, but there are also species of shrubs and succulents that grow in this habitat and therefore it is more diverse than the shrubland, which is dominated by shrubs and succulents (Richardson 1985). This difference in diversity of vegetation is reflected in the higher diversity of arthropods in the grassland than in the shrubland (Siemann *et al.* 1998). The pan, a habitat characterised by a depauperate plant community and very saline soil is the habitat with the lowest diversity. For most of the year the pan is either waterlogged or completely dry with hard soil and is therefore a very inhospitable environment of extremes affecting arthropod diversity negatively.

Each habitat type was more diverse during the dry season than during the wet season when ants were included in the analysis. Contrary to previous studies attributing the seasonal variation in arthropod diversity to rainfall, our results suggested that temperature had a significant influence (Buskirk and Buskirk 1976; Richards and Windsor 2007). Invertebrates have several adaptations to assist with survival when water is scarce, and in arid environments it can be expected that these animals are well adapted to deal with water restrictions (Danks 2007). Most previous studies have been in tropical regions where temperature remains fairly stable (Godfray *et al.* 1999). However, temperatures in our environment vary from extremely cold to very hot. Even though these animals will be well adapted to deal with water restrictions most arthropods have to remain dormant when the temperature drops, and in arid environments temperature will thus have a larger influence than in temperate regions (Danks 2007). Some species will still be able to deal with the extreme cold and will be active (Tigar and Osborne 1997). Since the Shannon-Weiner index is an index of heterogeneity, the activity of these few species will cause the dry season to be more diverse than the wet season. Ants are known as a species that occupy various niches and survive in various conditions in many habitats and as such they can be extremely dominant in any habitat type (Gibb and Cunningham 2011). When ants were excluded from the analysis there was less variation between habitat types, confirming that they had a large influence on alpha diversity in all habitat types.

Variation in beta diversity should be greater between different habitat types than within a specific habitat since arthropod communities develop within each habitat (Haddad *et al.* 2009). Due to these different arthropod communities, beta diversity will be directly influenced by habitat type as the habitat will determine which arthropods occur there (Humphrey *et al.* 1999; Ríos-Casanova *et al.* 2010). Arthropods tend to be active during the wetter months (Danks 2007), so beta diversity is higher during these months. Unlike alpha diversity, both temperature and rainfall influenced beta diversity, and the combination of these two factors played a larger role than habitat type on beta diversity as there was no significant difference between habitats during the same seasons. There is overlap in habitat types across Benfontein, and there should thus also be an overlap in arthropod communities as some species will be able to survive in more than one habitat type. However, even if a species occurs in more than one habitat type changes in rainfall and temperature will affect that species in all the areas it occurs in (Boyer *et al.* 2003; Danks 2007)

Habitat type did, however, play a significant role in the observed variation of arthropod abundance. The savanna provides a greater number of niches than the less complex pan which is an uninhabitable environment for much of the year, and furthermore the savanna provides more cover (Richardson 1985). Based on previous studies, the savanna should thus be the habitat type with the highest arthropod abundances (Deblauwe and Dekoninck 2007; Haddad *et al.* 2009; Haddad *et al.* 2001). Differences in the observed arthropod abundance between habitats were the same as the patterns of alpha diversity. Similarities such as these between alpha diversity and abundance have been observed before when the same habitats have been compared (Jonsen and Fahrig 1997). We therefore suggest that a considerable part of the variation in arthropod abundance and taxonomic composition is due to habitat structure and cover. It has been shown with both experimental and field studies that vegetation cover and composition of plant communities have a positive effect on the abundance of arthropods in grasslands (Crist *et al.* 2006; Perner *et al.* 2005). Our results are similar to other studies conducted in tropical areas where cover and forest floor mass has a positive effect on the number of arthropods (Sayer *et al.* 2010).

When ants were excluded from the analyses, the dry season savanna exhibited the highest abundance closely followed by the wet season savanna. Ants were the most commonly trapped arthropod in all habitat types, and in turn had a major influence on the numbers of arthropods trapped per habitat type, a common phenomenon due to the colonial behaviour of ants (Cheli *et al.* 2010; Seymour and Dean 1999). Ants tend to form foraging parties and consequently there is a good chance of trapping them in large numbers. Abundance of ants has also been shown to vary considerably across habitats and they can have a significant influence on the number of arthropods trapped in each habitat (Gibb and Cunningham 2011). The savanna was the only habitat type in which there were more arthropods caught during the dry season than in the wet season, a result that was not predicted. Previous studies (Barrow and Parr 2008; Boyer *et al.* 2003; Denlinger 1980; Wolda 1988) have also shown arthropods are more active during the wet season than during the dry season as found in the grassland, shrubland and on the pan, which may be explained by the predatory behaviour of ants. Ants are known to be predators of a variety of other arthropods that are more active after the wettest part of the year (Nelson *et al.* 2004). Just before the dry season and during the first stage of the dry season ants might thus become engaged in storing food items away and due to this it would seem like the dry season has more arthropods than the wet season (Deblauwe and Dekoninck 2007).

The savanna and the grassland show the highest similarity in composition of arthropod groups regardless of whether ants were included or excluded from the analysis. The grassland forms a transition zone between the shrubland and savanna and is thus more similar to both of them than they are to each other (Richardson 1985). The pan, which is geographically isolated from the savanna and grassland, shows the least amount of similarity to these habitat types. The pan, however, shares some characteristics with the shrubland, especially during the dry season. Both of these habitats are largely dominated by ants, a family that decreases greatly during the dry season. The number of ants again seem to be one of the major factors accounting for variations and similarities detected in this study. They are recognised as having a significant role in ecosystems as one of the major predators (Gibb and Cunningham 2011), and it is thus not surprising that they have such a major influence on arthropod diversity.

Seasons thus play a large role in the abundance of arthropods in this semi-arid environment, but of the seasonal effects, temperature seems to have a greater impact on arthropods activity than rainfall. It was confirmed by both indices of diversity as well as by abundance estimates that season had a significant influence on arthropods, but based on the results from the GLMM’s it appears that temperature has a greater influence than rainfall.

In contrast to previous studies in temperate and forest habitats (Dingle and Khamala 1972; Hails 1982; Janzen and Schoener 1968), temperature, rather than rainfall, seems to be the greater determining factor of diversity and abundance in this arid region, but more studies are need if this the same in other arid regions of South Africa. Habitat type and complexity still affected both diversity and abundance, as in all previous studies, but again it was temperature that affected the difference in diversity between habitats. We thus propose that in regions that are already devoid of water arthropods will be more affected by changes in temperature and change their activity patterns accordingly. Arthropods communities from drier areas thus seem to be better adapted to deal with dry months (Tigar and Osborne 1997). However, temperature will still have an influence on these animals and affect their activity patterns.

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~ Chapter 3 ~

Extension of the diet of an extreme foraging specialist, the aardwolf (*Proteles cristata*)+

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Abstract

The aardwolf, *Proteles cristata*, is a highly specialized myrmecophagous carnivore that feeds almost exclusively on termites of the genus *Trinervitermes*. Here we report data from an ongoing analysis of aardwolf diet, where we documented remains of sun spiders and scorpions in aardwolf scats. Although the prevalence of these items was low, with sun spiders recorded in nine and scorpion remains in one of 246 scats, our observations suggest that aardwolves opportunistically feed on larger prey than previously thought. However, our observations do not suggest that aardwolves utilized these large prey items as alternatives to their main food resource during periods of food scarcity. Therefore, we suggest that the adaptive advantages of such opportunism may be small, but that the observed behavioural plasticity could be advantageous under specific environmental conditions and therefore is maintained as a behavioural trait.

Key words: carnivore, solifugids, diet breadth, resource utilization.

Introduction

Mammal dietary strategies range along a gradient from generalist to specialist foragers. Generalists feed on a broad spectrum of dietary items approximately in proportion to their immediate availability (e.g. Reid *et al.* 1997), while species that exhibit specialized strategies use a restricted part of available food resources, and typically feed on these more than what would be predicted from their relative availability (Anderson & Erlinge 1977). Therefore, while the adaptive advantages of generalist strategies seem intuitive, the development and maintenance of specialist foraging strategies are puzzling (Abrahams 1987; Abrahams 1999; Fox & Vasseur 2008).

The aardwolf (*Proteles cristata*) is a small (5–10 kg) insectivorous hyaenid that is generally regarded as one of the most specialized foragers within the Carnivora (Koehler & Richardson 1990). There are two subspecies with separate distributional ranges in East and southern Africa. The diet has been quantified for both subspecies (Smithers 1971; Kruuk & Sands 1972; Cooper & Skinner 1979; Bothma *et al.* 1984; Richardson 1987b; Kok & Hewitt 1990; Taylor & Skinner 2000; Matsebula *et al.* 2009), with all studies indicating that aardwolves are extremely specialized and feed almost exclusively on one genus of termite, *Trinervitermes,* occasionally supplemented with the harvester termite *Hodotermes mossambicus* in southern Africa (Richardson 1987a). Other taxa of invertebrates that have been recorded in their diet include beetles (Coleoptera), ants (Hymenoptera: Formicidae), and other termite genera such as *Odontotermes, Macrotermes* and *Lepidotermes.* (Kruuk & Sands 1972; Cooper & Skinner 1979).

Sun spiders (Arachnida: Solifugae) and scorpions (Arachnida: Scorpiones) are commonly found in southern Africa (Dean & Griffin 1993; Griffin 1998;Leeming 2003), and form part of the diet of many birds and mammals (Arlettaz *et al.* 1995; Nel & Kok 1999; Kopij 2002; Kok & Nel 2004; Kopij 2005; Kopij 2007; Pietersen & Symes 2010). Sun spiders are not venomous, but they possess strong chelicerae and it has been suggested that they mimic the hiss of adders by stridulating (Hrušková-Martišová *et al.* 2008), both of which act as a defence mechanism against potential predators. Scorpions in southern Africa vary in venom strength from the highly venomous *Parabuthus* to weakly-venomed species of *Hodogenes*. As far as we are aware, there has been only one previous record of sun spiders in aardwolf diets (Smithers 1971), and no records of scorpion remains.

Here we present data on rare or unrecorded incidences of sun spiders and scorpions in the diet of aardwolves from central South Africa, and discuss these occurrences in the light of the dietary strategies of this highly specialized forager.

Materials and Methods

We conducted the study on Benfontein Game Reserve in the Northern Cape Province, South Africa (28°50’S, 24°50’E), between June 2008 and December 2009. We collected aardwolf scats weekly from middens located within the territories of ten radio-collared aardwolves. Although our study has suggested a substantial home range overlap in aardwolves, most of these ten animals had discrete ranges in relation to each other. We therefore believe that our scat analysis is reflecting the diet of at least

10 animals. Because the area has a distinct seasonal rainfall pattern, we divided each year into a wet and a dry season based on data received from the South African Weather Bureau, and scats were categorized by season. We randomly selected 246 of 521 collected scats, including 128 scats from the wet and 118 scats from the dry season.

We dried scats at 70°C for a period of 24 h and then washed them through a series of sieves to remove excess soil. We analysed washed scats for the presence of arthropod remains, such as termite and ant heads, beetle elytra and any other skeletal remains. To estimate the size of sun spiders and scorpions we measured the length of each sun spider chelicera and scorpion pincer recorded in scats. These were then compared to the same parts from intact specimens collected during a concurrent pitfall survey in the area.

Results

We found remains from the termite *Trinervitermes trinervoides* in all but one of the 246 scats analysed, supporting the expected dietary specialization of aardwolves within our study population. In addition we found remains of sun spiders in nine of the 246 scats (3.7%), and remains of scorpions in one scat (0.4%). Two of the scats containing sun spiders were collected during the dry season and seven during the wet season, while the scat containing the scorpion remains was collected during the wet season. The scats were collected from middens in the home ranges of five different aardwolves, suggesting that they may have been deposited by at least five individuals. The length of sun spider chelicerae varied from 3–5 mm, indicating that the individuals consumed were between 20 and 40m min length. The scorpion pincers were 8mm long which translates to a scorpion of about 70mm in length.

Discussion

Since both the scorpion and most of the sun spider remains were recorded in the scats from the wet season, which is when termites are most available as prey, our observations suggest that neither sun spiders nor scorpions were utilized as alternative prey during periods of food scarcity, but rather were consumed opportunistically. Since sun spiders are active and can deliver a painful bite (Leeming 2003; Hrušková-Martišová *et al.* 2008), it seems unlikely that they were ingested accidentally. We identified the scorpion as *Opistophthalmus* sp. (Scorpionidae). These scorpions are sit-and wait predators (Leeming 2003), similarly suggesting that their consumption was unlikely to be accidental.

Our observations suggest a degree of opportunism in aardwolf foraging behaviour, since both sun spiders and scorpions appear to have been actively preyed upon. Such opportunism can be regarded as adaptive if it helps specialized foragers sustain themselves during periods of food scarcity. However, these large prey items were consumed when the main prey items were most available rendering this explanation unlikely. Alternatively, behavioural plasticity in diet selection may be advantageous to individuals, since using a variety of food items may help individuals survive periods of food shortage, and may also be advantageous at other times, providing extra nutrition during, for example, breeding seasons. We therefore believe that such opportunism may be regarded as latent behavioural plasticity that may only become directly advantageous under specific environmental conditions, but is still retained within the population because it carries low evolutionary costs.

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~ Chapter 4 ~

Seasonal variation in the diet of a specialist, the aardwolf (*Proteles cristata*) and the impact of food intake on dietary competition[+]

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Abstract

We investigated seasonal variation in the diet of the aardwolf from an arid habitat in South Africa. Research has previously recorded dietary shifts in the aardwolf, whereas the currently study revealed that the aardwolves fed primarily on a single genus of termite, *Trinervitermes* spp., with greater than 95 % of their diet comprising termites of this genus being utilised during both the wet and dry season. We propose that below average rainfall in previous studies caused the changes in diet and this provides support for considering the aardwolf as an obligatory *Trinervitermes* specialist. In addition, we investigate the degree of dietary overlap between aardwolves and their heterospecifics by comparing the diets of these mammals which also partially supplement their diet with *Trinervitermes*. Our findings suggest that due to their specialisation aardwolves face minimal competition with other mammals.

Introduction

Diet influences a range of ecological variables such as habitat utilization (Duncan & Gordon 1999), home range size and overlap (Juarez & Marinho-Filho 2002), as well as inter- and intra-specific competition (Pianka 1974; Jaksić *et al.* 1980; Fedriani *et al.* 2000; Phillips *et al.* 2007; Svanbäck & Bolnick 2007). Amongst mammals, there are a variety of strategies for meeting energetic requirements and optimising feeding, often through either specialising on specific prey items, or adopting a more generalist diet (Carbone *et al.* 1999; Shipley *et al.* 2009). Within the order Carnivora most species are hunters or scavengers feeding on a variety of vertebrate prey, whereas only a few feed on plant matter (e.g. panda, *Ailuropoda melanoleuca*) (Mattson 1998) or insects (e.g. bat-eared fox, *Otocyon megalotis*) (MacDonald & Nel 1986; Nel & Mackie 1990), with many species being omnivorous with generalist diets (Kitchen *et al.* 1999; Juarez & Marinho-Filho 2002). Therefore, although many of the Carnivora have refined their diets to feed on meat, they tend to feed on a variety of species, and specialisation on a particular genus or family of prey items is rare (Elmhagen *et al.* 2000).

Prey availability can affect both the capture rate of specific prey items, and the total amount consumed (Thums *et al.* 2005; Murdoch *et al.* 2010). The functional response of a predator to prey density can be determined by comparing prey consumption with availability (Solomon 1949). Functional responses have been characterised into three types (Holling 1959). A linear response (Type I) is seen in filter feeders (Abrams 1984) when the predator consumes more prey as the prey availability increases; a decreasing curve (Type II) is found when a predator consumes prey at a decelerating rate as they increase in abundance, without switching to another prey when the main food source becomes limited (e.g. wolfs (*Canis lupus*) feeding on moose (*Alces alces*) (Hayes & Harestad 2000). The decrease in consumption rate occurs due to an increase in handling time until the predator is unable to consume more prey, or becomes saturated, and is commonly seen in specialist predators (Elmhagen *et al.* 2000; Křivana and Vrkoč 2004). A sigmoid response (Type III) is typically found when the predator switches between prey items and is more common in generalists such as Arctic foxes (*Alopex lagopus*) (Elmhager *et al.* 2000).

Prey availability often varies seasonally (Sovada *et al.* 2001), and this is particularly evident for Arthropoda. Arthropods are inactive during large parts of the year and in the arid regions of South Africa and they decrease in abundance during the colder, drier months (Chapter 2) (Boyer *et al.* 2003; Richards and Windsor 2007). Insectivores consequently face a particular challenge during low abundance, needing to feed on different prey types, by broadening their diet to compensate for the lack of prey. Specialist species, however, switch to different prey types less readily than generalist species (Murdoch 1969), creating a problem for species that specialise on seasonally variable arthropods, as they will either have to switch to an alternative food source or find another way to deal with the lack of prey.

Myrmecophages specialise on ants and termites, a diet with limited interspecific competition due to its low nutritional value (McNab 1984) but high seasonal variability (Redford 1983). Myrmecophagous mammals typically show little dietary variation, continuing to feed on either ants or termites or a combination regardless of the abundance of these arthropods (Milewski 1994, Abensperg-Traun 1991, McNab 1984). Myrmecophages are able to deal with these food restrictions due to a lower basal metabolic rate (BMR) than expected for their body mass (McNab 1984), enabling them to rely on a food source that is not appealing to most mammals. However, such a diet presents seasonal challenges in relation to prey availability.

The aardwolf (*Proteles cristata*) is an extreme specialist feeding almost exclusively on termites (Richardson 1987a), the only hyaenid showing specialisation (Cooper *et al.* 1999; Leakey *et al.* 1999; Maude 2005). Most of the aardwolf's diet comprises of a single genus of termite, *Trinervitermes*, with the particular species dependent on the geographic area in which the aardwolf occurs (Kruuk & Sands 1972; Bothma *et al.* 1984; Matsebula *et al.* 2009; de Vries *et al.* 2011). The soldiers of the *Trinervitermes* termites secrete a terpenoid-based substance used as a defence mechanism (Prestwich & Chen 1981; Breakman *et al.* 1984). This chemical has a marked odour and the secretions of the subfamily Nasutitermitinae may render them unpalatable to most predators (Lubin & Montgomery 1981), with only the aardwolf tolerating terpenoids at high concentrations (Richardson & Levitan 1994).

The aardwolf's diet of *Trinervitermes* is supplemented by *Hodotermes mossambicus*, another species of termite that forages above ground (Koehler & Richardson 1990; Uys 2002). The extent of diet switching by aardwolves is variable, with some studies showing a switch to *Hodotermes* during the dry season (Bothma *et al.* 1984; Richardson & Coetzee 1988), or conversely during the wet season (Matsebula *et al.* 2009), whereas others recorded little variation with season (Kruuk &

Sands 1972; Cooper & Skinner 1979). The change in diet has been attributed to the inactivity of foraging parties of *Trinervitermes* during the colder months of the year (Nel 1968b; Richardson 1985), indicating that aardwolves may be considered facultative specialists which are able to feed on other prey when their preferred prey is limited. Occasionally other prey items have been recorded, suggesting that aardwolves may be able to switch to another prey to compensate for the lack of *Trinervitermes* (de Vries *et al.* 2011).

With the exception of the aardvark (*Orycteropus afer*) few mammals in South Africa, other than the aardwolf, feed on *Trinervitermes*. A few other species consume *Trinervitermes* e.g. Pangolins (*Manis temmincki*), bat-eared foxes (*Otocyon megalotis*), yellow mongooses (*Cynictis penicillata*), black-footed cats (*Felis nigripes*) and Meller's mongooses (*Rhynchogale melleri*) (Taylor & Meester 1993; Swart *et al.* 1999; Stuart *et al.* 2003; Skinner & Chimimba 2005; Sliwa 2006), but only occasionally and, more importantly, in low numbers. The aardvark is the only mammal competitor of the aardwolf for *Trinervitermes*. There are birds that feed on *Trinervitermes*, but only occasionally. Conversely, several species of mammals feed on *Hodotermes mossambicus*, which may lead to increased competition during the dry months (MacDonald & Nel 1986).

In this study we investigate the changes in the diet of aardwolves across seasons using scat analysis and compare this to the abundance of prey items available. We use this to test the dietary response of aardwolves to changes in the abundance of their preferred prey, *Trinervitermes*, and subsequently determine the functional response shown by aardwolves to the abundance of prey. Since *Trinervitermes* *trinervoides* is largely inactive during the colder, dry months of the year, aardwolves may be under increased competition during this time, particularly if there are other mammals that also supplement their diet with *Hodotermes mossambicus*.

Materials and Methods

Study area

The study was conducted on Benfontein Game Reserve, in the Northern Cape Province of South Africa (28°50'S, 24°50'E). A large part of the reserve is covered by grassland and *Trinervitermes* mounds are common and widespread, creating an ideal habitat for aardwolves (Richardson 1985). The area is varied with a large pan section and many species of shrubs *Salsola exalata* and *Suaeda fruticosa*, therefore, it has a high diversity of invertebrates (Chapter 2), and their predators, such as yellow mongoose, bat-eared foxes and aardvark, which may be potential competitors for aardwolves.

Scat collection

Scats were collected between August 2008 and December 2010 from aardwolf middens located across the reserve. Most of these middens were located at night while tracking one of the five aardwolves via VHF transmitters placed on individual animals (see Chapter 5), and a few were found by walking through the reserve. Only fresh scats were collected and were placed in brown paper bags and labelled with the scat site code, date of collection and scat condition. These scats were either frozen at – 4 ^{o}C or immediately sun-dried to prevent bacterial degradation.

Based on data received from the South African Weather Bureau the scats were separated into those collected during the wet and the dry season. Wet season was defined as months that received more than 40 mm of rain and stretched from October to March, whereas the dry months was from April to September. A total of 637 scats were collected from 16 middens, and from these we randomly selected a subsample of 246 samples covering 15 months (eight in the wet season and seven in the dry) to be analysed by numbering each scat and using a random number generator to select scats. A total of 128 scats were analysed during the wet season and 118 during the dry season. The large number of samples makes this the most comprehensive study on aardwolf diet to date.

Scat analysis

Scats were oven dried for a period of 24h at 70 °C and the dry-weight recorded (Table 5, appendix) (Dickman & Huang 1988). Each scat was subsequently washed through a series of mesh sieves (grid size 500 µm and 250 µm) to remove soil from the scats. The scat samples were dried for a second time and weighed to obtain an estimate of the amount of sand and dirt that was present in each scat, since aardwolves ingest sand while foraging (Richardson 1987b). The entire scat was analysed and investigated for the presence of arthropod remains such as termite and ant heads, beetle elytra and solifugid mandibles.

We devised a new method to quantify the relative contribution of different diet categories in insectivore scats from a subsample of the scat, designed to enhance reliability of analysing entire scats by selecting random subsamples more accurately. Each scat was placed in a 10 cm x 10 cm x 2.5 cm container and mixed with water until the entire scat had a fluid consistency. A grid was then placed in the container dividing the scat into 25 blocks, each with dimensions of 2 cm x 2 cm x 2.5 cm and the container was placed back into the oven for a period of 24h at 70 ° C for drying. Previous methods that selected a subsample of a scat to analyse also mixed the scat with water and then took a sample from this mixture, but since some items are denser than others and because some particles float to the top, our method allows all items to settle and spread evenly before a dried sample is taken. We selected five scats containing different varieties and numbers of prey items to analyse in full. This was done in order to determine how many subsamples would be required to provide a reliable estimate of the number of prey items per scat. We used 1000 Bootstrap replications on each prey item and each scat, and found that five blocks (20 % of each scat) were sufficient to estimate the number of all prey items per scat. The prey items used for the Bootstraps were based on those found during the binomial analysis. These five blocks were randomly selected by numbering each block and used R 2.13 (The R Foundation 2011) to choose random blocks, and all arthropod remains in these blocks were counted. Remains of arthropods were separated into eight categories: 1) *Trinervitermes* soldiers and 2) workers, 3) *Hodotermes*, 4) *Odontotermes*, 5) ants, 6) beetles, 7) solifugids and 8) scorpions, which represented the prey items found in the binomial analyses. For all termite genera and ants we used head capsules as an indicator for the presence of one individual. The number of Coleoptera was estimated by dividing the number of elytra by two, the number of solifugids per scat was estimated based on number of mouth parts found per scat and the number of scorpions by number of pincers.

Prey abundance

Once a month three pitfall traps were placed at six random sites in each of the four habitat types found on the Reserve and left in the field for seven days. To ensure that specimens could not escape, traps were half filled with a 2:1 mixture of water and propylene glycol. After traps were collected from the field, specimens were placed in 70 % ethanol to be analysed at a later stage. All of the prey items found in the scats, namely *Trinervitermes* sp., *Hodotermes* sp., *Odontotermes* sp., Formicidae, Coleoptera, solifugids and scorpions were removed from the traps and counted.

Statistical analysis

We determined the mean number and the mean percentage of individual prey items found per scat, as well as the mean number and the mean percentage of prey items per pitfall trap for each month. We plotted both variables from the scat data against those obtained from the pitfall traps in order to test which data gives the best resolution of the data, which showed that plotting the mean percentage of prey items found per scat against the mean number of prey items found in the pitfall traps gave the best fit. For percentage prey items per scat we used the mean percentage per month and used a Kruskal-Wallis non-parametric ANOVA with post-hoc Wilcoxon matched paired test with a Holm correction for multiple comparisons to determine if there was a significant difference between the percentages of prey items. To assess if there was a significant difference in the mean number of prey items per trap the same test was used as for the percentage prey per scat. We tested for differences in the number of prey items in both the scats and traps between months with single sample t-tests.

We subsequently fitted the three types of functional response curves as proposed by Holling (1959) to the data. The type I model was fitted using a linear model (Scat.Perc = Trap.Nr) using the percentage of prey items in scats as the response variable (Scat.Perc) and the mean number of prey items caught in pitfall traps as the predictor variable (Trap.Nr). For both the type II and type III responses we used the Levenberg-Marquardt nonlinear least-squares algorithm (Banks *et al.* 1987) applying the minpack.lm package in R 3.0 (The R foundation for statistical computing). The algorithm for the Type II functional response was in the format (Scat.Perc = (a x Trap.Nr) / (b + Trap.Nr)) where the values for parameters a and b were the best match between the model and the observed data. The algorithm for the Type III functional response was similar but with an added parameter ‘c’ (Scat.Perc = (a^c x Trap.Nr^c) / (b^c + Trap.Nr^c)). The response curves were evaluated based on AICc values using a 7 delta AIC cut-off instead of the normally used 2 delta to delineate support for each model in order to ensure model accuracy. For functional response analysis we grouped *Odontotermes*, solifugids and scorpions into one catergory namely "Other" due to the low numbers in which they were consumed.

Frequency of occurrence (FO) and percentage contribution (PC) were used to estimate the importance of prey items in the diet during each season and to investigate variation in diet across season. FO was determined across season by dividing the number of scats containing a specific prey species by the total number of scats collected for each month. The Wilcoxon matched paired test with a Bonferroni correction for multiple comparisons was used to test for significant differences in FO of prey groups between the wet and dry season during each month scats were collected. PC was determined for each month by dividing the number of individuals from a specific prey group found in all the scats from that month by the total number of prey items found and multiplying this by 100. This allowed us to test for variation across seasons. Again, Wilcoxon matched paired tests with a Bonferroni correction were performed to test for differences in the PC of each prey item and in diet composition between seasons.

In order to test for differences in the diversity of prey items between the wet and dry season we used the Shannon-Wiener index of diversity with PRIMER software version 5.2. From the Shannon- Weiner Index an H score is obtained which gives an indication of alpha diversity. A higher H score is an indication of higher diversity. This was done both for PC and FO using a Wilcoxon matched paired test to test for significant differences between the wet and dry season for both PC and FO.

Results

Aardwolf diet

Both workers and soldiers of *T. trinervoides* were present in all of the 246 scats analysed, with 13 containing only *T. trinervoides* while 83 scats consisted of a combination of the three termite genera, namely *T. trinervoides*, *H. mossambicus* and *Odontotermes* spp., but no other items. Therefore, 39% of scats contained only termites (96/246), indicating that aardwolves do feed on other prey items regularly but not necessarily in high numbers. Sand formed a large part of all scats with 41 % (STD 42%) comprising of sand, which is consumed as a by-product while aardwolves lick up termites.

T. trinervoides was the most commonly consumed prey item with an FO of 100 % during both the wet and dry season (Fig. 1), and little variation between seasons when the PC of each prey item was considered (wet 98.3%, dry 94.6 %, Fig. 2). There were more soldiers than workers eaten during both the wet and dry seasons (3.5 % more during the wet season, 4.5 % more during the dry season). No prey items were consumed in higher numbers during any specific season compared to the other season (Table 1). The second most commonly consumed prey item was *H. mossambicus*, but in much smaller quantities (FO: wet 50.9 %, dry 49.5 %, Fig. 2; PC: wet 1.02 %, dry 4.62 %, Fig. 2) than *T. trinervoides*. There were no significant differences in the consumption of any prey items between seasons (Fig. 2 & Table 2). All other prey items, except *Trinervitermes trinervoides* and *Hodotermes* *mossambicus*, contributed less than 1 % to the total diet in both the wet and dry season.

The Shannon-Wiener Index showed that the diversity of arthropods consumed varied little between the wet and dry season when PC is considered, although the dry season was slightly more diverse (H Score = 1.14) than the wet season (H Score = 1.08). However, when the FO was considered, the wet season (H = 1.42) was more diverse than the dry season (H = 0.97), but based on the Wilcoxon matched paired test the differences were not significant.

During the wet season, *Odontotermes* spp., *Hodotermes mossambicus*, solifugids and scorpions were trapped more frequently (df = 9, t = 4.52, $p < 0.05$; Coleoptera : df = 9, t = 8.66, $p < 0.05$; Other: df = 9, t = 2.36, $p < 0.05$). Formicidae, Coleoptera and “Other” were trapped significantly more during the wet season than during the dry season (Formicidae: df = 9, t = 3.09, $p < 0.05$; Coleoptera: df = 9, t = 6.79, $p < 0.05$; Other: df = 9, t = 4.46, $p < 0.05$)

We detected a variation in the numbers of *Trinervitermes* and *Hodotermes* trapped across months (*Trinervitermes:* mean = 3.26, STD = 0.69; *Hodotermes* mean = 7.19, STD = 1.09) but were trapped in small numbers. There was a significant difference between the number of prey items trapped (Kruskal Wallis ANOVA: χ^2 = 39.08, df = 4, $p < 0.05$). Numbers of *Trinervitermes* and *Hodotermes* trapped differed significantly from those prey items belonging to the Formicidae and Coleoptera (Fig 3) based on the post-hoc Wilcoxon matched paired test (*Trinervitermes* : Formicidae $p < 0.05$; *Trinervitermes* : Coleoptera $p < 0.05$; *Hodotermes* : Formicidae $p < 0.05$ *Hodotermes* : Formicidae $p < 0.05$). All “Other” prey types where trapped in relatively small numbers (3.46 STD = 0.24) and also only differ significantly from Formicidae and Coleoptera (Formicidae $p < 0.05$; Coleoptera $p < 0.05$). Formicidae were trapped in the highest numbers (495.96 STD = 50.60) and were trapped significantly more than any other prey items (Wilcoxon matched paired test: *Trinervitermes* $p < 0.05$; *Hodotermes* $p < 0.05$; Formicidae $p < 0.05$; Coleoptera $p < 0.05$). Coleoptera were the second most commonly trapped of all the prey items (83.95 STD = 3.91).

For both of the main prey items, *Trinervitermes* and *Hodotermes*, the data follows a type I functional response. This was also the case for prey in the Formicidae even though it did not differ much from a type II response based on the AICc values (Table 3). The consumption of Coleoptera is best described by a type II response, but again it did not differ from either the type I or type III functional responses. All ‘Other’ prey items followed a type III response but this did not differ much from the type I & II responses.

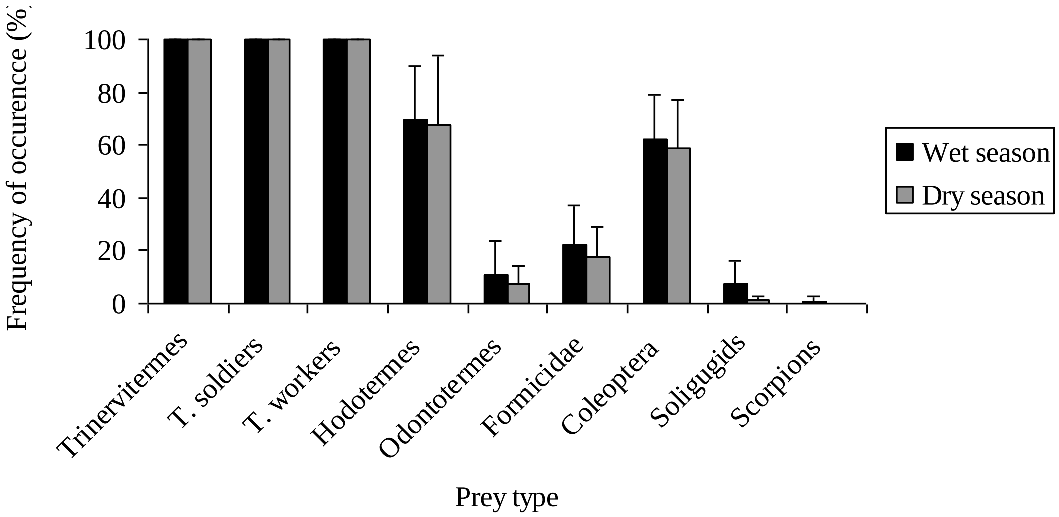

Figure 1. The monthly frequencies of occurrence of the major prey items found in scats of aardwolves collected during the wet and dry seasons. Error bars show standard deviation.

Prey item	N	Z	p
H. mossambicus	5	0.4	0.68
Odontotermes sp	5	0.4	0.69
Formicidae	6	1.4	0.17
Coleoptera	6	0.52	0.6
Solifugids	4	1.1	0.27
Scorpions	1	0	1

Table 1. Wilcoxon matched paired test results of the comparison of frequency of occurrence of prey items between the different seasons. No significant differences were found.

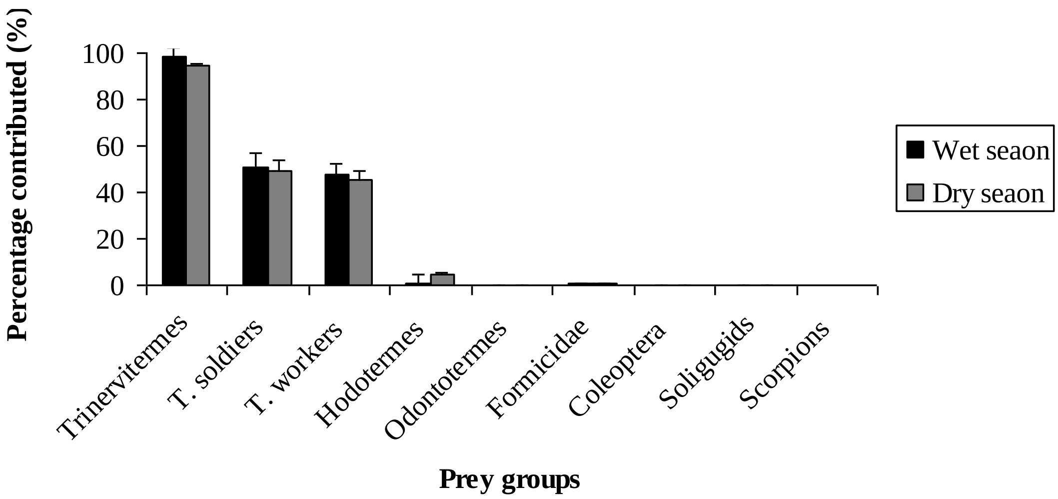

Figure 2. Proportions of arthropods that contributed to the total number of prey items detected in aardwolf scats. Error bars indicate standard deviation between the months of each season.

Prey item	N	Z	p
T. trinervoides	7	1.9	0.06
T. trinervoides Soldiers	7	1.35	0.17
T. trinervoides Workers	7	0.17	0.86
H. mossambicus	7	1.86	0.06
Odontotermes sp	6	0.31	0.75
Formicidae	7	1.18	0.23
Coleoptera	7	0.34	0.73
Solifugids	2	0.71	0.48
Scorpions	1	0	1

Table 2. Wilcoxon matched paired test results of the comparison of percentage contribution of prey items between the different seasons. No significant differences were found.

Prey species	FR Type	Equation	Delta AICc
Trinervitermes	I	Scat.Perc = Trap.Nr	0.00
	II	Scat.Perc = (100 x Trap.Nr) / (3 + Trap.Nr)	697.02
	III	Scat.Perc = $(100^1$ x Trap.Nr$^1) / (3^1$ + Trap.Nr$^1)$	703.02
Hodotermes	I	Scat.Perc = Trap.Nr	0.00
	II	Scat.Perc = (80 x Trap.Nr) / (20 + Trap.Nr)	8.09
	III	Scat.Perc = $(100^5$ x Trap.Nr$^5) / (0.1^5$ + Trap.Nr$^5)$	385.7
Formicidae	I	Scat.Perc = Trap.Nr	0.00
	II	Scat.Perc = (15 x Trap.Nr) / (0 + Trap.Nr)	3.88
	III	Scat.Perc = $(20^1$ x Trap.Nr$^1) / (0^1$ + Trap.Nr$^1)$	10.19
Coleoptera	I	Scat.Perc = Trap.Nr	0.03
	II	Scat.Perc = (60 x Trap.Nr) / (0+ Trap.Nr)	0.00
	III	Scat.Perc = $(60^1$ x Trap.Nr$^1) / (0^1$ + Trap.Nr$^1)$	4.96
Other	I	Scat.Perc = Trap.Nr	1.12
	II	Scat.Perc = (40 x Trap.Nr) / (0 + Trap.Nr)	3.06
	III	Scat.Perc = $(40^1$ x Trap.Nr$^1) / (0^1$ + Trap.Nr$^1)$	0.00

Table 3. Functional response models for each prey category with comparative AIC values for each of the three types of models.

Discussion

Even though extreme dietary specialisation in carnivores is rare (Adam & Mitchell 2009), we can confirm that aardwolves are one of the most extreme specialist feeders relying almost entirely on one genus of termites. *Trinervitermes* was the predominant prey resource consumed during wet and dry seasons, although few scats contained only this genus. Other prey types consumed on regular occasions, but in much smaller quantities, which might indicate that they are fed on accidentally while the aardwolf forages on termites.

The large foraging parties formed by *Trinervitermes* and *Hodotermes* (Uys 2002), present an abundant food source that, when available, requires little handling time. However, during winter these arthropods are largely inactive (Braack 1994) and consequently aardwolves need to feed on alternative food resources during these times, yet they do not switch their diet during the winter. Instead aardwolves reduce their activity in order to conserve energy and may lose up to 20% of their body mass as their subcutaneous fat deposits become depleted (Anderson 2004; Richardson, 1985, 1987a). They also lower their body temperature by up to 6 ^{0}C at night during winter to conserve energy (Anderson 2004), and readily share dens with other individuals in order to conserve heat (Richardson, 1985; Anderson, 1994).

While aardwolves are specialists relying on one genus of termites for most of their nutritional needs, they are also somewhat opportunistic, feeding on other prey items when they come across them. However, they do not seem to actively seek them out, since alternative prey items only increase in the diet when their abundance increases (reflecting a Type I and Type II functional response). In most vertebrates the expected functional response is either a type II response for specialist animals or a type III for generalists (Andersson & Erlinge 1977). Our results indicate that aardwolves follow a type I response for both of their two main prey items and show no distinct switch in their diet regardless of the abundance of *Trinervitermes*.

The consumption of both Formicidae and Coleoptera increases as they increase in abundance, indicating that aardwolves do feed on these opportunistically while foraging. The 'Other' prey items consumed by aardwolves included termites from the genus *Odontotermes* and two arachnids (solifugids and scorpions). *Odontotermes* are wood-feeding termites (Uys 2002) and are thus rarely found above ground which makes them mostly unavailable to aardwolves. Both solifugids and scorpions would appear to be a good food source due to their larger sizes. However, solifugids are fast-moving with a painful bite, whereas scorpions are venomous, both posing potential dangers to aardwolves (Leeming 2003). These defensive mechanisms force aardwolves to either expend more energy to capture and feed on these arthropods or risk obtaining a painful bite or potentially harmful sting. Aardwolves can feed on other arthropods (de Vries 2011), such that it is intriguing that they undergo such physiological stress during the colder months of the year instead of incorporating more prey items in their diet. It is, however, possible that the energetic costs of searching for alternative prey would be too high to be profitable for aardwolves and that they thus rather spend more time conserving energy.

Most mammalian myrmecophages have low basal metabolic rates (BMR) compared to other mammals (McNab 1984) and the BMR of the aardwolf is low for its body size (Anderson 1994). The reduced BMR would thus give aardwolves a means to survive the winter months by drawing on fat reserves built up during the warmer periods. The use of these fat reserves is the cause of the severe body mass lost during the winter months (Anderson 2004). It is possible, however, that the reported 20 % of body mass loss during winter is not as physiologically stressful as it might first appear, especially since the first scat deposited at night can weigh more than 1 kg (J.L. de Vries, *pers obs*), equating to more than 10 % of the animal's body mass.

Feeding on a diet of *Trinervitermes* will result in less competition with other, less specialist animals. The only other mammal on Benfontein Game Reserve that regularly feeds on these specific termites is the aardvark (Appendix, Table 4)(Willis et al. 1992; Taylor *et al*. 2002). Bat-eared foxes and yellow mongooses also prey on *Hodotermes* regularly and might thus compete with aardwolves during the dry season (Bothma *et al.* 1984; MacDonald & Nel 1986; Nel & Mackie 1990; Kok 1996), but aardwolves did not switch to a diet of *Hodotermes mossambicus* and it is unlikely that they compete with these species.

The terpenes used as a defence mechanism by *Trinervitermes* dictate that only a few species of mammals utilise them into their diet (Richardson 1987a) and should thus exclude aardwolves from competition with terpene-intolerant species. In turn, aardvarks forage by digging into the centre of termite mounds to feed on the larvae and alates, leaving an abundance of adult termites for aardwolves to feed on (Taylor *et al.* 2002). Aardwolves may, therefore, benefit from foraging aardvarks rather than competing with them for this food resource. This is supported by observations of aardwolves following aardvarks and eating the termites from mounds aardvarks opened while foraging (Taylor & Skinner 2000). During the summer months

Trinervitermes are active above ground and abundantly available (Adam *et al.* 2008) and so aardwolves will benefit most from aardvarks opening mounds during winter.

In summary, in the Northern Cape Province of South Africa aardwolves specialise on a diet of *Trinervitermes trinervoides* and supplement this diet mainly with a limited number of *Hodotermes mossambicus*. Aardwolves thus appear to be obligatory specialists that will continue to feed on one genus of termite regardless of the abundance of the termites. Even if this specialisation reduces competition from other species of myrmecophage, the aardwolves' inability to switch to another prey type causes them to lose body mass during winter which in turn increases pup mortality (Richardson 1985; Anderson 2004). Other prey items, such as Formicidae and Coleoptera, were found, but in very small numbers. However, when the sizes and nutritional value of these other prey items are considered, it is possible that they contribute more to the diet than the scat analysis reveals. Further studies are necessary to confirm if aardwolves compete with other animals, including birds and invertebrates for food resources.

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Appendix

	Prey items		
Mammal species	***T. t.***	***H. m***	**Other prey items and reference**
Aardwolf	100 %	100 %	Only invertebrates (Cooper & Skinner 1979)
	100 %	11 %	Only invertebrates (Cooper & Skinner 1979)
	100 %	36.5 %	Only invertebrates (Cooper & Skinner 1979)
	100 %	12.5 %	Only invertebrates (Cooper & Skinner 1979)
	96.9 %	1.9 %	Only invertebrates (Bothma *et al.* 1984)
	89 %	46 %	Mostly invertebrates (Kok 1996)
Aardvark	15 %	8.5 %	Mostly Formicidae (Willis *et al.* 1992)
	15.3 %	2.9 %	Mostly Formicidae (Taylor *et al.* 2002)
Bat-eared fox	1 %	93 %	13 % vertebrates (Stuart *et al.* 2003)
	18.2 %	81.8 %	Only invertebrates (Bothma *et al.* 1984)
	5 %	54 %	Mostly invertebrates (Kok 1996)
	0 %	95 %	Mostly invertebrates (MacDonald & Nel 1986)
	0 %	69.1 %	93.5 % invertebrates (Nel & Mackie 1990)
Yellow mongoose	0 %	57 %	Invertebrates (90% - 100%, some vertebrates (40.8 % - 10.3 %) (Anderson *et al.* 1997)
	0 %	17.5 %	
	0 %	51.3 %	91. 2 % invertebrates (Avenant & Nel 1997)
	0 %	90 %	48 % mammals (MacDonald & Nel 1986)
Black-footed cat	0 %	> 1 %	99 % vertebrates (Sliwa 2006)

Table 4. Frequency of occurrence of *Trinervitermes trinervoides* (***T. t***) and *Hodotermes mossambicus* (***H. m***) in the diet of aardwolf and findings for four other species that co-habit with aardwolves on Benfontein Game Reserve.

Scat number	Weight	Scat number	Weight	Scat number	Weight	Scat number	Weight
1	237,2	63	254,2	125	286,8	187	112,0
2	194,4	64	646,6	126	622,7	188	285,2
3	163,7	65	26,1	127	181,1	189	76,0
4	172,5	66	116,7	128	613,9	190	439,5
5	275,9	67	25,1	129	503,5	191	185,9
6	99,2	68	346,9	130	1003,8	192	398,4
7	535,0	69	311,7	131	346,2	193	184,2
8	664,1	70	549,2	132	491,6	194	175,7
9	43,1	71	392,7	133	359,4	195	488,9
10	60,8	72	370,5	134	405,2	196	352,6
11	119,3	73	169,4	135	391,1	197	373,9
12	132,4	74	319,3	136	563,1	198	182,7
13	667,6	75	49,6	137	350,9	199	180,8
14	77,2	76	150,2	138	369,0	200	303,9
15	226,3	77	156,6	139	161,2	201	306,0
16	957,3	78	87,9	140	489,6	202	438,6
17	418,0	79	355,2	141	200,4	203	145,2
18	48,2	80	229,9	142	383,4	204	238,9
19	31,3	81	50,5	143	181,5	205	80,0
20	208,8	82	153,8	144	494,5	206	107,8
21	68,5	83	10,5	145	451,5	207	134,1
22	83,6	84	292,2	146	388,3	208	182,4
23	81,9	85	24,5	147	565,4	209	174,0
24	569,1	86	18,1	148	698,1	210	78,8
25	234,7	87	106,5	149	74,4	211	102,8
26	201,0	88	348,3	150	161,1	212	241,5
27	247,5	89	270,0	151	131,1	213	237,3
28	360,4	90	140,8	152	328,7	214	91,2
29	306,5	91	140,4	153	114,4	215	284,5
30	403,6	92	95,4	154	250,1	216	233,7
31	192,6	93	235,3	155	338,1	217	114,0
32	146,7	94	160,0	156	751,0	218	46,2
33	351,1	95	145,9	157	209,7	219	307,8
34	82,2	96	218,9	158	78,0	220	92,8
35	16,2	97	814,4	159	138,4	221	209,0

36	18,5	98	427,7	160	141,3	222	77,5
37	438,0	99	147,9	161	132,8	223	128,2
38	284,1	100	323,5	162	125,8	224	151,9
39	441,0	101	471,4	163	383,4	225	50,0
40	135,1	102	122,7	164	38,4	226	245.95
41	89,9	103	170,2	165	55,5	227	161.44
42	72,3	104	32,5	166	345,3	228	223.91
43	28,9	105	89,3	167	244,6	229	35.4
44	45,7	106	355,5	168	124,2	230	274.6
45	61,9	107	707,5	169	49,5	231	161,1
46	88,7	108	223,8	170	591,9	232	319,3
47	61,9	109	356,8	171	207,3	233	74,4
48	519,5	110	53,8	172	370,2	234	83,6
49	67,6	111	33,3	173	78,7	235	306,0
50	26,1	112	59,5	174	187,4	236	114,4
51	167,7	113	345,1	175	79,0	237	355,5
52	67,2	114	51,0	176	49,3	238	32,5
53	40,7	115	68,5	177	548,8	239	138,4
54	37,5	116	63,6	178	316,5	240	82,2
55	30,8	117	11,2	179	563,2	241	25,1
56	9,2	118	164,5	180	67,2	242	238,9
57	33,5	119	549,5	181	148,3	243	32,5
58	73,6	120	49,0	182	241,5	244	646,6
59	151,5	121	383,8	183	1045,9	245	549,5
60	192,0	122	304,9	184	447,6	246	388,3
61	26,5	123	593,1	185	134,8		
62	54,7	124	645,4	186	424,4		
Total mean :	**241,9**				**Standard deviation :**		**198,0**

Figure 5. Dry weights (g) of all scat samples analysed with mean weight and standard deviation.

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~ Chapter 5 ~

The influence of prey abundance on home range size of an extreme diet specialist, the aardwolf +

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Abstract

The effect of the abundance of prey on home range size in a population of aardwolves was investigated in the Northern Cape Province of South Africa. Aardwolves are highly specialised and feed predominantly on a single genus of termites, *Trinervitermes* spp. The density of termite mounds of the prey species was compared to the size of home range in five (two male, three female) individual aardwolves. We show home range overlap and the sharing of dens by male individuals, a phenomenon previously undescribed. We found a mean home range size of 3.47 km^2 (SD 1.93) with home range sizes varying between 1.39 km^2 and 5.53 km^2. Aardwolf home range sizes varies according to the density of termite mounds with smaller home ranges possessing a higher density of termite mounds than larger home ranges. The sizes of mounds do not have an influence on the size of home ranges. No aggressive behaviour was observed and individual aardwolves appear more tolerant to neighbouring conspecifics than previously thought.

Introduction

Prey availability has a wide range of effects on mammals influencing factors such as diet (Cantú-Salazar et al., 2005; Delibes-Mateos et al., 2008), choice of den locations (Szor, Berteaux & Gauthier, 2008) and the space used by the animal (Eide, Jepsen & Prestrud, 2004). The availability of food resources is a primary factor influencing the use of space in a wide variety of taxa (Macdonald, 1983; Carr & Macdonald, 1986). In the Carnivora, the size and use of home ranges is affected by prey abundance as well as both their temporal and spatial distribution. Empirical support for prey abundance as a driver for size of an area used by an animal has been found in a number of species of solitary carnivores such as the Eurasian lynx (*Lynx lynx*) (Schmidt, 2008), mountain lion (*Puma concolor*) (Grigione *et al.*, 2002) and bobcats (*Felis rufus*) (Knick, 1990).

The size of an area used by a particular carnivore is also influenced by the prey type hunted by that carnivore species and the way in which it captures the prey (Mauritzen, Derocher & Wiig, 2001; Weckel, Giuliano & Silver, 2006). The insectivorous species within the Carnivora should theoretically require a smaller home range than meat-eating species of the same size, since their source of protein is more locally abundant (Gittleman & Harvey, 1982). Consequently two species of Carnivora, the European badger (*Meles meles*) and coyote (*Canis latrans*), which are of similar size (approximately 13 kg) occur at very different densities, probably due to their prey type (Carbone & Gittleman, 2002). The European badger feeds on a wider variety of prey ranging from invertebrates to vertebrates compared to the coyote which is primarily a hunter of mammals.

Since larger animals have higher absolute energy requirements and thus need larger areas to sustain themselves, body size can impact space use (McNab, 1963; Schoener, 1968; Gittleman & Harvey, 1982; Kelt & Van Vuren, 1999). The relationship between body mass and home range size has been well documented for mammals using all feeding strategies, including the insectivores, herbivores, carnivores and omnivores (Harestad & Bunnel, 1979; Gittleman & Harvey, 1982). Most insectivores will consume a variety of arthropods and do not specialise on one specific taxa (Kruuk & Parish, 1981; Dickman & Huang, 1988; Joshi, Garshelis & Smith, 1997). The few animals that do specialise on a specific taxon, such as myrmecophages (animals that feeds on ants and termites), will thus, not necessarily behave as predicted by the energetic models proposed by Gittleman & Harvey (1982) as these animals rely heavily on a specific prey type, and will have larger home ranges.

Overlap in the space use between sexes has been observed in a number of carnivores, and individuals of the same sex will often tolerate home range overlap with conspecifics, depending on the mating strategy (McCarthy, Fuller & Munkhtsog, 2005; Jiménez, 2007; Cavalcanti & Gese, 2009). However, spatial overlap between animals is dependant on the distribution of food resources in the area and, where prey items are clumped, animals tend to overlap more than when items are evenly distributed (Eide *et al.*, 2004). When prey items are unevenly spaced or scarce, individuals need to defend these resources and will then form territories and display aggressive behaviour towards other individuals.

The aardwolf is regarded as a highly specialised carnivore and its diet has been well studied by previous authors (Smithers, 1971; Kruuk & Sands, 1972; Cooper & Skinner, 1979; Bothma, Nel & Macdonald, 1984; Richardson, 1987b; Matsebula *et* *al.*, 2009; de Vries *et al.*, 2011). The effect of variations in abundance and availability of their main prey source, the termite *Trinervitermes* spp., on the size of home ranges has never been investigated. Due the importance of *Trinervitermes* in their diet (Cooper & Skinner, 1979), it is reasonable to assume that all predictions on home range size relating to prey abundance should be based on the availability of these termites. Therefore, I test a) whether the abundance and distribution of *Trinervitermes* within a home range relate to home range size, and b) whether there is a difference in the size of termite mounds between the different home ranges that will influence the number of termites available. Lastly, I test whether home range boundaries overlap with those of neighbouring aardwolves, and compare these results to previous studies.

Materials and Methods

The study was conducted on Benfontein Game Reserve (28°50'S, 24°50'E) north of Kimberley in the Northern Cape Province of South Africa. Between February 2008 and January 2010 a total of 11 aardwolves (seven males, six females) were captured by darting from a vehicle at night and subsequently fitting a radio collar (Sirtrack Ltd, Havelock North, New Zealand: weight 68.25 ± 8 g, mean ± 1 SD placed around the neck. The aardwolves were anaesthetised using a combination of 36 mg ketamine hydrochloride and 0.6 mg metotomedine choride using a CO_2 powered injection rifle (Dan-Inject JM standard, Skellerup, Denmark, or Telinject G.U.T, Römerberg, Germany) at distances of between 11 and 15 metres (Anderson & Richardson, 1992). The metotomedine was subsequently reversed using 3.0mg atipamezole hydrochloride. All animals were fully mobile within 90 minutes from initial injection. Two of these animals lost their collars, two died and radio contact was lost with a further two. The other five individuals were habituated by waiting for them to emerge from their dens in the evening and following them by vehicle. Animals were initially followed at a distance of 50 m or greater as this did not appear to influence the behaviour of the animal, since the aardwolves continued foraging without paying much attention to the vehicle. Once animals were habituated they could be followed in a vehicle at night at a distance of between 10 and 20 m while the animal kept on foraging. Each individual was followed for six nights a week, over a 23 month period, and during each night the time of initial encounter until the time of departure from the animal was recorded. This was done to ensure that animals were not followed at the same time during the same week so that a bias for a specific time period was not created. During this time accurate GPS locations were obtained on all of these animals as they traversed the reserve. A location was recorded when the animal was seen for the first time each night. In the case where the animal was still in its den the GPS location of the den was used.

The GPS way points were plotted in ArcGIS 9.3.1 (1999 – 2009 ESRI Inc.) and used to construct home ranges using 95% Minimum Convex Polygons (MCP) for all 11 animals (Burt, 1943; Hayne, 1949). We used 95% MCP as this method is more robust and it would enable us to compare the data to previous studies. Bootstrap analysis was conducted using ArcView GIS 3.3 (1992 – 2002 ESRI Inc.) (Appendix 1), indicating that at least 55 locations were needed per animal to accurately determine the home range size. We collected between 115 and 62 waypoints on five of the collared animals. Consequently only enough GPS locations were obtained for five out of the 11 animals and seasonal variation could not be determined. Number of waypoints required differed depending on the size of the home range. Even though there were only enough way points to accurately determine home range size for five animals, I was still able to detect the areas that animals overlapped in with the 95 % MCP. For ease of interpretation, however, not all the 95 % MCPs are displayed on the same map. The home ranges for all animals for which enough waypoints were obtained were plotted onto one map and all other animals on a separate map.

The number of termite mounds was used as a proxy for the number of termites available as a food resource to the aardwolves. *Trinervitermes* spp. construct epigeal mounds when they are active in an area (Uys, 2002), and more *Trinervitermes* spp. actively forage in areas with higher mound density (Richardson 1985). Termite mound density was determined by walking a 100 m transect from 10 randomly selected points within each home range. Distance analysis was subsequently used to estimate the number of mounds within each home range using the software DISTANCE (Thomas *et al.*, 2009b). Mounds were counted up to a distance of 50 m on either side of the transect line and therefore each transect covered an area of 1 ha and a total of 10 ha in each home range were sampled. This method of sampling was used as it adheres to the requirements of the software to accurately determine home range sizes. DISTANCE allows the user to determine the density of animals or objects based on transect or point data. Based on Uniform, Half-normal and Hazard-rate key functions and Cosine, Simple polynomial and Hermite polynomial series expansions the software uses the distance and angle from the transect or point to give an estimate of the density of objects which is extrapolated to a larger area (Buckland *et al.*, 2001; Thomas *et al.*, 2009a). Conventional distance sampling (CDS) was used as I assumed that the detection of all mounds on the transects was certain (Thomas *et al.*, 2009a). All the key functions and series expansions were tested and model performance was assessed using Akaike Information Criterion (AIC), so that each key function was run with each of the three series expansions and in total nine models were tested. Based on the AIC values each model was run using a Uniform key function with a Cosine series expansion. These models were used to determine the density of termite mounds for each transect, within each home range and across the entire Reserve. Variation between transects was determined with single sample t-test, using density determined in each transect. The variation between home ranges was determined with Kruskal-Wallis ANOVA’s as the estimate home range sizes were non-parametric. A linear regression was used to test whether the number of termite mounds within a home range affects home range sizes.

Measurements of the radius (r) and height (h) of the first ten termite mounds of each transect were taken to obtain an estimate of the volume of the mounds as it has been shown that mound volume affects number of termites in an area (Josens & Soki, 2010). Assuming that the mounds of *Trinervitermes* are cone-shaped the volume for each mound was calculated using the formula $V = {}^{1}/_{3}\, \pi\, r^2\, h$. The estimated volume was compared to previous studies (Richardson, 1985) that have determined the number of termites present within a mound of a specific size. We tested for differences in mound sizes between home ranges using Wilcoxon signed rank test with continuity correction. The mound volumes were also used in conjunction with termite mound density in a Generalized Linear Model (GLM) with a Poisson error distribution and log function to test which of these two factors had the largest impact on home range size. The interaction between mound density and volume was included in the model and a type II ANOVA was used to test for significance.

Results

Based on the MCPs, the five aardwolves which had sufficient way points to categorically define the home range had an average home range size of 3.47 km^2 (SD 1.93). There was, however, large variation in home range size with the largest home range occupied by Male 8 (5.53 km^2) and the smallest by Female 7 (1.39 km^2, Table 1).

The density of mounds within each animal's home range varied significantly between the 10 transects within each home range (**F6**: t = 4.14, df = 9, p = 0.003, **F7**: t = 4.79, df = 9, p = 0.001, **F9**: t = 2.65, df = 9, p = 0.026, **M2**: t = 3.50, df = 9, p = 0.007, **M8**: t = 2.81, df = 9, p = 0.020), but there was no significant difference in the density of termite mounds between any of the home ranges of individual animals. A significant inverse relationship (r^2 = 0.97, n = 5, p = 0.01) was, however, found between the size of home ranges and the density of termite mounds within that home range. The volumes of mounds in the home range of Male 2 differ significantly from those of the animals geographically furthest away from each other, namely Female 6, Male 8 and Female 7 (Wilcoxon rank test: M2-F6: n = 68, z = 3,104060, p = 0,001909; M2-M8: n = 57, z = 2,935754, p = 0,003328 ; M2-F7: n = 70, z = 4,415472, p = 0,000010). The same pattern was observe for Female 9 which differ significantly in the sizes of mounds from Female 6 and female 7 (Wilcoxon rank test: F9-F6: n = 65, z = 1,963748, p = 0,049560; F9-F7: n = 65, z = 3,388364, p = 0,000703). Linear regression indicated that there were no correlation between mound volumes and the size of the home range (r^2 = 0.209, n = 5, p = 0.439). The GLM confirmed that mound density influenced home range size, even though the results only approached significance (df = 1, F = 88.91, p = 0.06). The interaction between mound density and mound volume (df = 1, F = 9.98, p = 0.19) and mound volume itself were not significant (df = 1, F = 0.02, p = 0.91).

Overlap in home ranges of these five animals was observed: home ranges of Female 6 and Male 8 overlapped considerably, and both of these animals overlapped with Female 9 to the west of their respective home ranges whereas Female 6 overlapped slightly with Female 7 to the east. Male 2 overlapped with Female 9 in the eastern part of his home range (Fig. 1).

Figure 2 depicts potential "home range" areas used by individuals for which there was a deficiency of data as indicated by the bootstrap analysis. This Figure therefore does not indicate home range overlap since these areas cannot be referred to as home ranges, but rather areas that were used by more than one individual. Male 2 left his home range in the west (labelled Male 2 A in Fig. 2) and moved to the eastern part of the reserve for a period of two months. During this time his "home range" overlapped with that of Female 1 (Fig. 2, Male 2 B). Before he moved, Male 2 shared parts of the area that he occupied in the eastern part of the farm with Male 3 and Male 4 (Fig. 2). Male 3 was followed for less than two months and Male 4 for just over a month before both of them lost their collars, and therefore it was not possible to accurately determine their "home ranges". While all three of these animals were being followed it was found that they shared dens on five nights. Male 3 shared a den with Male 2 on two occasions and with Male 4 once. Male 4 also shared dens with Male 2 on two occasions. This is the first time that den sharing has been recorded between male aardwolves.

Individual	**95% MCP**	**Mound density (number/km^2)**	**Mean Mound Volume (STD)**
Female 6	3.96 km^2	1706	95.94 l (87.26)
Female 7	1.39 km^2	8751.1	104.26 l (87.77)
Female 9	3.75 km^2	2866.4	62.30 l (53.63)
Male 2	2.70 km^2	4033.2	49.44 l (44.15)
Male 8	5.53 km^2	720	87.83 l (73.03)
Mean	3.47 km^2	3615.3	79.98 l

Table 1. Home range sizes (95 % MCP) and mound density per km^2 of the five aardwolves for which sufficient data were collected.

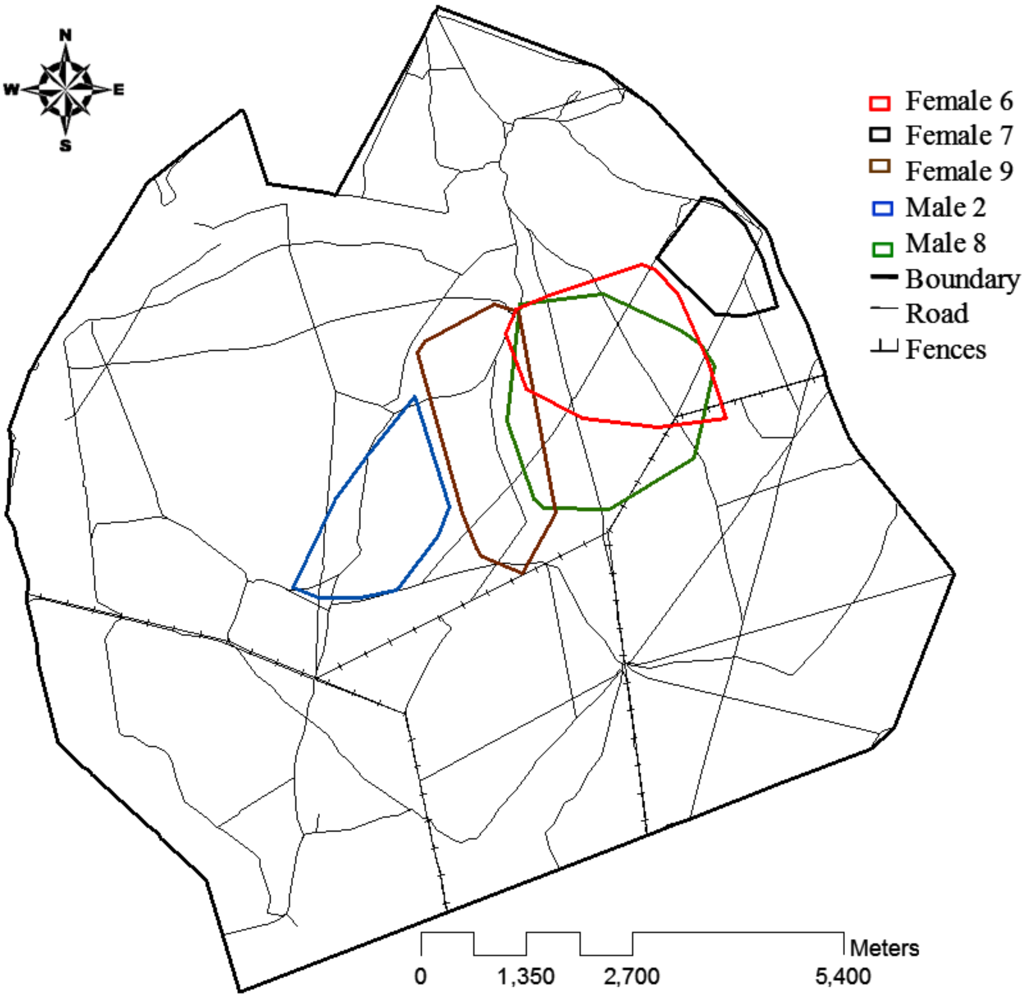

Figure 1. Home range (95 % MCP) of the five aardwolves for which sufficient data were collected to accurately estimate home range sizes.

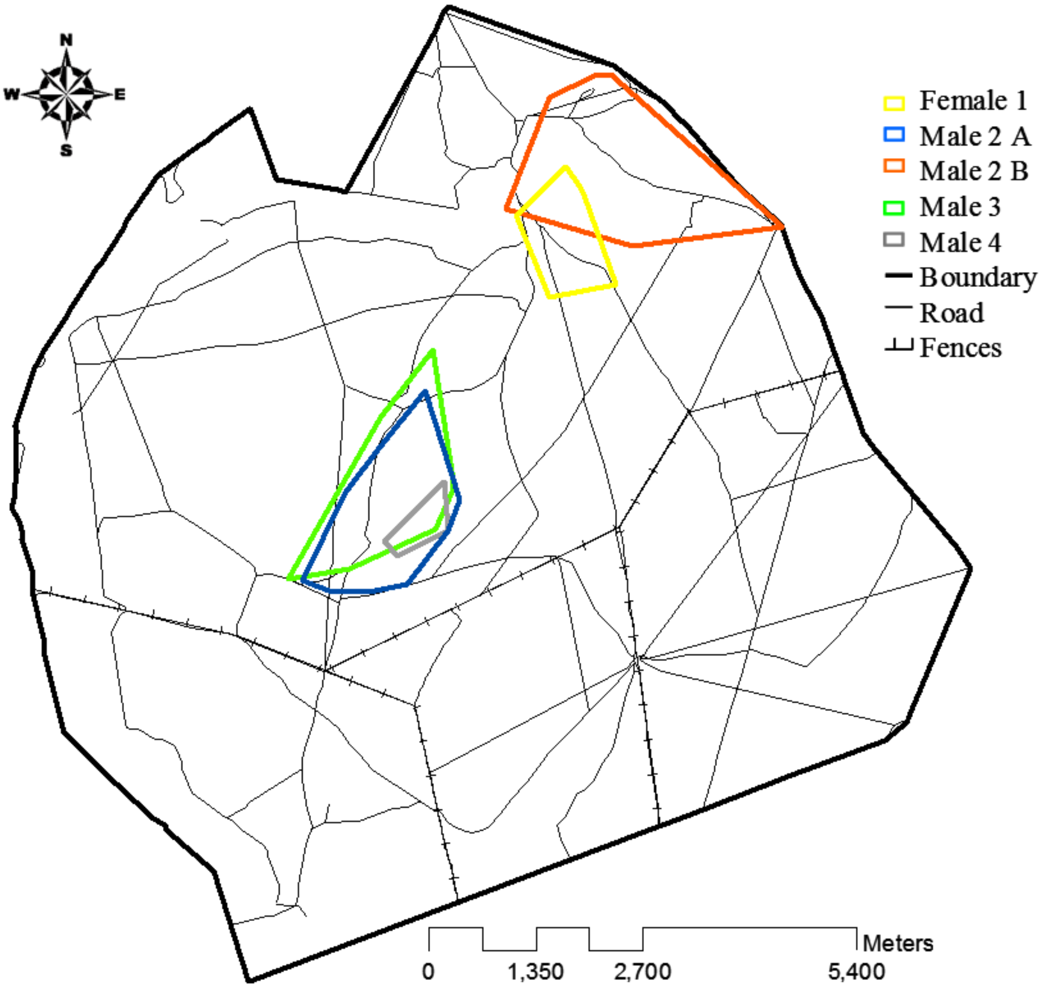

Figure 2. Home ranges (95 % MCP) of five aardwolves which had overlapping "home ranges" but for which there were not a sufficient number of way points to accurately determine home range sizes.

Discussion

Home range sizes of aardwolves varied greatly, although the range and mean size are similar to those previously reported by Skinner and van Aarde (1985), but larger than those found by Richardson (1985) at the same locality as used in this study. Skinner and van Aarde (1985) proposed that aardwolves need an area of 4 km^2 based on the density of aardwolves and the size of home ranges in Rustenburg Nature Reserve, but this was based on a single female’s home range.

We propose that the variation detected was due to the density of termite mounds, and hence the availability of food available to the territory holder. The size of home ranges increased as the density of termite mounds decreased in a curvilinear fashion suggesting that aardwolves in the area maintain a home range that is of a size that contains a sufficient number of termite mounds to sustain their energetic requirements. Richardson (1985) also proposed that variation in home range size was due to food resource availability, but also stated that territoriality played a role in home range size. While our results do not exclude competition and territoriality as factors, we never observed any aggressive or territorial behaviour between neighbours. In addition, we found overlap in home ranges between neighbouring individuals, suggesting that home ranges were not defended or exclusive.

The overlap detected in home ranges during this study contrasts with Richardson (1985) who found that the home ranges of a male and female pair overlap entirely. He proposed that this home range have exact boundaries which do not overlap with that of the neighbouring male and female, which will again keep and defend their own territory. During our study there was no indication of home range boundaries and individuals overlapped. Contradictions in home range use between studies on the same species are not uncommon in the literature: (Dietz, 1984) found that maned wolves (*Chrysocyon brachyurus*) defended a territory from other individuals whereas (Jácomo *et al.*, 2009) reported that there was considerable overlap in the spatial distribution of maned wolves. Jácomo *et al.* (2009) proposed that these overlaps may be due to higher prey abundance which resulted in occupants of a territory becoming more tolerant towards conspecifics as has been observed in arctic foxes (*Alopex lagopus*), where home ranges were more spread out with less overlap when food sources were scarce, but overlapped more when food was abundant (Eide et al., 2004). The same rationale could be applied to aardwolves: when aardwolves occupy an area where termites are abundant they will allow other individuals to enter into their home range.

During the course of Richardson's study in 1985 there was a severe drought across South Africa which was reportedly the worst in 60 years (Lund, 1983). Richardson (1985), who conducted his study in the same area as the present one, stated that termite mounds started dying off during the time he conducted the study. During the time that the present study was conducted, there was a 50 % increase in rainfall compared to this previous study (South African Weather Bureau). Droughts such as these have may be the major reason for a large scale die-off of termite mounds by Coaton (1948) (cited in (Nel & Malan, 1974). It is thus not unreasonable to assume that during the time our study was conducted there was a higher abundance of termites than during the study conducted by Richardson (1985), which would bring about a reduction in territoriality by aardwolves to protect this food resource.

Based on the theoretical home range models for carnivores ($H = 0{,}11W^{1.36}$) where H is home range size and W the mass of the animal (Harestad & Bunnel, 1979) the expected home range size for aardwolves is predicted to be 2.52 km^2 (10 kg, (Koehler & Richardson, 1990). This is an under-representation of the home range sizes we found, but larger than home range sizes recorded by Richardson (1985). Gittleman & Harvey (1982) stated that based on their model, insectivores have surprisingly small home ranges, a result they attributed to their protein-rich diet making them efficient feeders. However, the availability and distribution of the food source will still influence the home range. This is confirmed by the relationship between the size of home ranges and the number of termite mounds found in those home ranges. The more dispersed the food resources are, the larger the area that aardwolves have to travel to find food (e.g. Male 8). If termite densities are sufficiently high, aardwolves may be able to have smaller home ranges as they do not need to travel long distances to find sufficient resources.

Even though mound sizes were significantly different between a few home ranges there was no relationship found between the size of home ranges and the size of mounds. Considering that termite density per mound decrease per mound size unit (Josens & Soki, 2010) we can assume that larger mounds will not necessarily equate to more termites and that a more accurate measure of termites available would be number of mounds.

The overlap that we found in home ranges may be attributed to prey availability, but this does not explain the sharing of dens between males. Unfortunately not enough data was gathered on these individuals to confirm if dens were shared seasonally, and thus we could not confirm if this was just huddling behaviour. A possible reason for den sharing by males is the formation of coalitions, although further research is required to confirm this statement. Coalitions have, to our knowledge, never been reported in aardwolves prior to this study, but this is also the first time that adult aardwolves of the same sex have been seen to den together. Aardwolves are thought to be socially monogamous (Richardson, 1987a), and only on one occasion have two males been reported to occupy the same territory (Richardson, 1985). A recent study suggests they are sexually polygamous based on den use (Kotze *et al.*, 2012). However, no den sharing between these males was reported. Male coalitions have been found in a relative of the aardwolf, the striped hyena (*Hyaena hyaena*) (Wagner *et al.*, 2007; Wagner, Frank & Creel, 2008), and other hyenas are social (Smith *et al.*, 2008). The reasons behind the formation of coalitions are often difficult to determine (Olson & Blumstein, 2009) and more research needs to be undertaken to determine if this occurs in aardwolf populations and what the role of these coalitions are, both in terms of relatedness of the individuals and the sex composition.

In conclusion, we have shown that the size of aardwolf home range was negatively related to the density of termite mounds, but not related to mound size. This study provides evidence that specialised animals such as myrmecophages might adjust their home range sizes according to the availability of prey than maintaining strict territories. The reasoning behind this statement comes from comparisons of the results from this study to those of Richardson (1985) who found territorial behaviour between individuals. The overlap detected in this study indicates that these animals are more tolerant of conspecifics when more resources are abundantly available.

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~ Chapter 6 ~

General conclusion

I present the most comprehensive study on the feeding biology and spatial ecology of the aardwolf undertaken to date. I have confirmed the importance of *Trinervitermes trinervoides* as the primary dietary item for the aardwolf and shown that they rely completely on these termites and do not show a switch to other prey regardless of their abundance. In addition I have demonstrated the extent to which the presence and abundance of *T. trinervoides* can influence the size of the home range that aardwolves occupy. Based on predictive models, aardwolves are theoretically too large to be able to sustain themselves on termites alone (Carbone *et al.* 1999, Carbone *et al*. 2007), and yet the abundance of termites dictate many aspects of their ecology.

The Northern Cape Province of South Africa is characterised by sporadic and unpredictable rainfall events as well as large daily temperature fluctuations which may present inhabitants with difficult conditions. In this arid environment, it is temperature rather than rainfall which affects the abundance and diversity of arthropods (Chapter 2). This contrasts with studies conducted in temperate and forest habitats where it has been found that rainfall has a more significant impact than temperature (Dingle & Khamala 1972; Hails 1982; Janzen & Schoener 1968). Few studies have surveyed the abundance and diversity of arthropods in arid environments and as a consequence this study is highly valuable, particularly considering the dependence of a number of vertebrates on the arthropod assemblage as a primary food resource. Four species of large mammals (aardwolf, aardvark, bat-eared fox and yellow mongoose) rely on diets that comprise predominantly arthropods. This does not include the many other smaller mammal species, birds and reptiles that also rely on arthropods. Understanding variability in arthropod abundance and diversity, and the underlying causes of these variations, are crucial to investigating the ecology of all these vertebrate species. With this study I broaden our understanding of arthropods in the arid regions of South Africa, and present results that can be used for comparison in all arid regions of the world.

Arthropod abundance is lower during the dry season and a specialist termite feeder, such as the aardwolf, would be expected to switch to an alternative prey species or incorporate more prey items into their diet to compensate for this lack of preferred food resource. As part of my research into the diet of the aardwolf I designed a new method for scat analysis, that I deem to be more accurate than previously used for insectivores, and this indicated that aardwolves do not switch to alternative prey regardless of the abundance of termites (Chapter 4), despite having access to other potential invertebrate prey items (Chapter 3). I was the first to show that aardwolves do not switch to a different food type with season and that they follow a Type I functional response, which is rarely recorded in mammals where generally a Type II or Type III functional response is found depending on whether they are specialists (Type II) or generalists (Type III, Abrams 1984; Elmhager *et al.* 2000; Hayes & Harestad 2000). A Type II functional response is seen when the consumption of a prey item increases exponentially as that prey item increases in the case of specialist mammals where the only reason for slow consumption rate at low densities is search and handling time. A type III functional response is seen when a generalists switch to a prey type when it reaches a certain density. Aardwolves depend almost exclusively on a single genus of termites, *Trinervitermes*, with as much as 98.3 % of the diet comprising this food commodity, and show a linear increase in the numbers consumed compared to the numbers available. Aardwolves show no switch in diet with season and continue to feed on *Trinervitermes* even when the food resource is less active during the colder months. With this study I have demonstrated that a Type I functional response is found in aardwolves, and that this functional response could thus be found in mammals. I propose that the reason for this functional response in aardwolves is that there is a minimal handling time by aardwolf on termites. Once found, termites are readily consumed and require little handling, due to the large groups that they form while foraging. The diets of other myrmecophages have been investigated (Abensperg-Traun 1991; Redford 1983; Redford 1986), but no previous study has investigated functional response or prey abundance, and it is thus possible that other mammalian myrmecophages may also follow a Type I functional response. All myrmecophages feed on a prey item that occurs either in large nests or forms large foraging parties, and as such handling time of prey is minimal (Redford 1983), however, without data on prey abundance it is not possible to determine if they do.

I was the first to demonstrate that aardwolves feed on scorpions, and one of few to show that solifugids are incorporated into the diet, revealing that they are capable of feeding on a much larger variety of prey (Chapter 3). Anderson & Jordaan (1991) state that aardwolves are incapable of feeding on vertebrate prey due to an inadequate dentition, but a recent publication has shown them to feed on captive geese (*Anser anser domesticus*) (Yarnell & MacTavish 2013). Aardwolves may thus be capable of feeding on a much wider variety of prey than was previously thought, however, instead of incorporating more prey items into their diet during the dry months aardwolves lower their basal metabolic rate and lose as much as 20% of their body mass (Anderson 2004). Not only is this a physiologically stressful time but during this time pup mortality is higher than the wet months (Anderson 2004).

The areas that are occupied by aardwolves are highly influenced by the density of *Trinervitermes*, and my research shows a strong correlation between the sizes of an aardwolf's home range and the number of termite mounds in the area. Home range sizes are however, larger than would be expected for an animal of that size (Harestad & Bunnel, 1979), and this is possibly to ensure there is enough of a food source available (Redford & Dorea 1984), or to ensure adequete mating opportunities. In another myrmecophage, the short-beaked echidna (*Tachyglossus aculeatus*), home range sizes are smaller than what would be predicted by the size of the animal (Nicol *et al*. 2011). This discrepancy in report of home range size is very likely due to the abundance of a suitable prey source in the area, and it is thus possible that aardwolf home ranges will vary across South Africa depending on the abundance of *T. trinervoides*.

A comparison of the results from this study with those of a previous study by Richardson (1985) has shown that the abundance of *Trinervitermes* plays a crucial role in the defence of the home range. I found no evidence of aggressive behaviour between aardwolves and in fact I found that there is considerable overlap in home range between neighbouring individuals. In marked contrast, previous studies report that aardwolves only overlap with one member of the opposite sex and that they defend the boundaries of their home range religiously (Richardson 1991). This is contradictory to my findings and this may be attributed to the lower abundance of *Trinervitermes* recorded as a result of reduced rainfall experienced during the period of the previous work done (Lund 1983).

Considering these findings on the importance of a specialised diet on aardwolf ecology, more intensive studies are needed on mammalian myrmecophages and the relationship between these mammals and their main diet. For many myrmecophages the diet has been determined such as the silky anteater (*Cyclopes didactylus*, Best & Harada 1985), the banded anteater (*Myrmecobius f. fasciatus*, Calaby1960) and the giant anteater (*Myrmecophaga tridactyla*, Naples 1999) but even this fundamental part of their ecology is not known for all of these specialists. Functional responses have never been explored with respect to changes in diet with the availability of prey and thus not understood well enough at this stage. My research has shown what a substantial impact the abundance and diversity of prey can have on these mammals and will hopefully lead to more in depth research on a wider variety of myrmecophages.

In a few myrmecophagous mammals home range sizes have been investigated, such as the giant anteater (Medri & Mourao 2005) lesser anteaters (*Tamandua tetradactyla*, Rodrigues *et al*. 2001), and the short-beaked echidna (*Tachyglossus aculeatus*, Nicol *et al*. 2011), but none have linked this to the abundance of prey items. Sprent & Nicol (2012) have shown that habitat type influences home range sizes of short-beaked echidnas, but suggested that this is due rather to restrictions of shelter available than prey abundance. Similar to aardwolves, short-beaked echidnas also have home ranges that are smaller than expected from their body mass (Nicol *et al*. 2011), but this analysis has not been done on other myrmecophages. Cape pangolins (*Manis temminckii*) show an increase in home range sizes as body size increases (Heath & Coulson 1997), but these were never compared to home range size of other myrmecophages, and all other pangolin species have been poorly studied. Male Cape pangolins show overlap with other male individuals, but this overlap is small compared to the overlap they show with females (Heath & Coulson 1997). Aggressive or defensive behaviour has never been observed in any other myrmecophage, which implies that Richardson (1991) has the only home range defence observations on myrmecophages. This again may be attributed to the potential lower abundance of termites during the time his study was conducted. It is thus possible that other myrmecophages will defend home ranges when prey abundance is low.

Little work has been published on the behavioural ecology of aardwolves and likewise certain aspects of the ecology of the aardwolf are poorly understood. My thesis has shown that there is a degree of overlap between neighbouring aardwolves which is in conflict of the finding of a previous study (Richardson 1985) suggesting that the abundance of *Trinervitermes* may dictate if aardwolves defend a home range from conspecifics or whether they will tolerate home range overlap. I demonstrated that den sharing between male individuals indicate the possibility that coalitions may arise between close relatives. Coalitions have never been reported in aardwolves, but a relative of the aardwolf, the spotted hyaena (*Crocuta crocuta*) is a social mammal (Smith *et al*. 2005) and coalitions have been found in the striped hyaena (*Hyaena hyaena*), another hyaena that is behaviourally solitary as the aardwolf (Wagner *et al*. 2008). Coalitions have been reported in a number of members of the Carnivora, and seem to be formed when males try and monopolise breeding rights with females or enhance their chances of breeding success, increase hunting success or to defend a territory or to take remove a dominant male from a group (de Villiers *et al*. 2003, Mills *et* al. 2004, Waser *et al*. 1994). Since aardwolves do not need to hunt their prey, show overlap in home ranges and do not form groups or packs the only explanation for the possible coalitions are to obtain access to females. Further studies are needed to assess how aardwolves regulate their home range and whether they do indeed exhibit coalitions.

Richardson (1987) and Richardson & Coetzee (1988) have suggested cuckolding behaviour in aardwolves, but there has been no definitive study to investigate mate choice. I found no evidence of cuckolding, but my data indicates significant overlap, making it a possibility, since animals will be able to come into contact with members of the opposite sex. Males gain benefit from cuckolding by having another male raise its offspring, but few studies have investigated female preference in extra pair copulations. Nothing is known about the mating behaviour of aardwolves. Kotze et al. (2012) showed that aardwolves are probably polygamous through extra pair copulations based on den usage. However, through genetics we will be able to better determine if male aardwolves do mate with more than one female and if it is possible for one male to be dominant in an area and possess mating rights with many females.

Prey abundance is known to influence the fecundity of a number of mammals (Ward *et al*. 2009, Samelius *et al*. 2011), and it has been shown that a lower prey abundance affects reproduction rate of mammals negatively. The effect that the abundance of *Trinervitermes* has on the survival rate of adult aardwolves and their fecundity has never been studied. Since *Trinervitermes* plays such an active role in all the known aspects of aardwolf ecology it is predicted that the abundance of the termites will determine the survival of adults and the number of pups that are produced per year. Pup mortality increases when *Trinervitermes* abundance decreases during the drier months (Richardson 1985, Anderson 2004), but the long term effect of reduced termite abundance has never been investigated. This can only be assessed by long term monitoring of aardwolf populations and the associated *Trinervitermes* densities and abundance over time.

Few other mammals are as highly specialised and selective in their diet as the aardwolf (Redford 1987), and it has been shown that mammals with specialist diets have a higher extinction risk compared to other mammals (Harcourt *et al*. 2002; Boyles & Storm 2007). No studies to my knowledge have ever linked myrmecophage specialisation to potential risk of extinction, and at present the aardwolf does not appear to face such a risk. However, considering that my results indicate that in arid environments arthropod abundance are influenced by temperature and that predictive modelling show that the arid environments of South Africa will generally experience higher temperatures and aridification will increase (Kruger & Sekele 2013), aardwolves might face a decrease in food availability due to climate change. This is not specific to aardwolves, since other animals depend on arthropods and will also be influenced by a decrease in their abundance. For another specialist in the order Carnivora, the giant panda (*Ailuropoda melanoleuca*), it is speculated that climate change will affect their food abundance, and this species may also become more threatened due to changes in climate and consequently changes in vegetation structure (Tuanmu *et al*. 2013). Taken into context the climate change predictions will have dramatic consequences on the distribution and survival of many insectivorous species, including the aardwolf, where a change in arthropod density and assemblage will have a direct effect on several mammals higher in the food pyramid. In order to assure that these animals are conserved more studies are need to determine the effects that prey abundance can have on mammals.

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